On the assembly of a grassland plant community

Thesis

On the assembly of a grassland plant community

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Some general notes

Statistics

Statistical calculations for this thesis were undertaken using MINITAB except the generalized linear model fitted in Chapter 5 for which STATISTICA was used.

Many of the statistical tests involve multiple comparisons. In order to guide the judgement when assessing statistical probability, at the foot of each table I have given the adjusted probability value (Bonferroni's correction) for the series of tests nominally applied at the 5% level. I have not adjusted the tabulated values themselves because the Bonferroni correction can lead to an excessively conservative test. Instead, I have regarded any results at between the tabulated 5% level and Bonferroni corrected value as being marginal.

Nomenclature

In matters of taxonomic nomenclature, I follow Kent (1992) throughout this thesis.

Abbreviations

Some frequently used abbreviations in this work.

ANOVA - analysis of variance

MANOVA - multivariate analysis of variance

NVC - National Vegetation Classification (Rodwell 1992)

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Abstract

The species pool for a site is defined as that set of species which have a non-zero probability of maintaining viable populations under the prevailing environmental conditions. It may contain many more species than are actually present in the community of the site. The science of community assembly attempts to understand how particular communities arise from the welter of possible species combinations.

The assembly of a grassland plant community from the local species pool was examined in a phylogenetically corrected trait-based study. Competition theory suggests coexisting species should be less similar than expected by chance, whilst environmental sorting theory suggests they should be more similar. This work suggests that, at the whole community scale, species tend to be more similar and that their likelihood of occurrence in communities can to an extent be predicted from their traits.

Experimental studies revealed a complicated picture. Species naturally occurring in the community did not show convincing signs of outperforming their absent congeners. Community composition appears to depend in considerable measure upon chance events such as seed dispersal coinciding with the availability of vacant microsites in the community, rather than just a sorting process in which the best suited species are invariably present.

These findings suggest that it modelling community assembly is possible, but that it is unlikely ever to be an exact science because it is influenced to a large extent by unpredictable events.

Chapter 1. Introduction

1.1 Objectives and general introduction

In this thesis I investigate the assembly of a grassland plant community. I try to discover why it contains the species that it does, and examine how this information might be used to model the assembly of communities in general rather than just this one in particular. Biologists have long been convinced that communities of organisms are not just random collections of species (e.g. Raunkiaer 1934), and for over two decades (e.g. Diamond 1975) ecologists have attempted to model the way in which the actual community arises from the welter of possible species combinations. The study and modelling of community assembly is a central theme in ecology (Drake 1990) and is of much more than just theoretical interest (Keddy 1992, Kelly 1996, Thompson *et al.* 1996). Issues relating to environmental change and its effects on earth's biota (including mankind) are now of very general concern, and the need to predict changes in communities following changes in environmental conditions has never been greater (e.g. Smith *et al.* 1997). Two key questions are: *i)* is it possible to predict how the species composition of a community will change when subject to a specified change in environmental conditions? ("response rules", Keddy 1992), and *ii)* if so, what is the most reliable way of doing so? As a first step, we may begin with well-studied communities and, working backwards, attempt to discover why they are composed of a particular set of species. Only when we can account for the organisation or assembly of extant communities can we hope to predict future changes. Some progress has been made in this (see section 1.3), but many difficulties remain. I briefly review these matters below.

1.2 The fundamental basis of assembly models

All attempts to model community assembly have in some way been built upon a foundation of non-randomness. Communities, it is shown (or assumed), are not merely haphazard collections of species, but are organised in some way which may be identified and, to a greater or lesser extent (one hopes), understood. It is this non-randomness that enables predictions to be made, and the further the species composition departs from randomness, the more readily it may be detected and predictions made. The claim that communities are non-random assemblages of species is surely one of the least controversial claims that an ecologist might make. Keddy (1992) argues that this has been adequately proven and that it is time to move on to other problems. It does, however, beg the question 'non-randomly assembled with respect to what?' Communities may be examined at different scales (e.g. Wilson and Watkins 1994, Thompson *et al.* 1996, Diamond 1975, Cornell and Karlson 1996) and various types of process may operate upon the species which together form the community (e.g. Scarsbrook and Townsend 1993, Poff 1997, Diamond 1975, Cody 1991, Herrera 1992, Silvertown and Wilson 1994). There is, therefore, the potential for communities to depart from random species combinations in different ways according to the scale under investigation and the process being studied. In my opinion this has not received the attention it deserves, but is an essential consideration when one is attempting to model community assembly.

1.3 Conflicting predictions from ecological theory

There are two contrasting ecological traditions regarding the types of non-randomness which may be observed in community assembly from a set of potential colonists. The first asserts that competition is of fundamental importance in shaping community composition and, in its classical form, states that competition is greatest between those species which are

most similar (e.g. Darwin 1902: pp 93-96). This was investigated and found to be the case by Johansson and Keddy (1991). The corresponding prediction is that the most stable (and therefore the most likely to be observed) community arises when coexisting species are least similar. In several cases where this hypothesis has been examined, statistically significant effects tending to support the theory have been observed (e.g. Wilson and Watkins 1994; Wilson and Gitay 1995) although such effects have at times proved elusive (e.g. Wilson *et al.* 1996a).

There is, however, an equally long-standing tradition in ecology and phytogeography (e.g. Raunkiaer 1934, Schimper 1903) which regards species in communities as being more similar to one another than would be expected by chance. This similarity is considered to result from environmental influences such as climate acting upon species which are constrained in terms of evolutionary possibilities: there are fewer 'solutions' to ecological problems than there are species. Under a given set of environmental conditions, only those species possessing the right set (or sets) of attributes will be able to establish themselves in the community (e.g. Montalvo *et al.* 1991). Coexistence of similar species has also more recently been suggested on competitive grounds (Aarssen 1984) in contrast to the classical theory of competition expressed by Darwin.

These two schools of thought lead to quite opposite predictions about the sorts of species which comprise communities. Given this apparent contradiction and the fact that the fundamental ideas have such a long and eminent ancestry, it is all the more surprising that attempts to investigate community structure by way of species' characteristics almost invariably make reference to one or other but rarely both (although see Cody (1991) for a noteworthy exception). The two contrasting types of prediction are examined in Chapter 3, and an attempt to reconcile these ideas is made in Chapter 8.

1.4 Previous attempts at modelling community assembly

Early empirical attempts to model community assembly were applied to avian communities. Diamond (1975) investigated the assembly of bird communities on islands in the New Guinea region. He asked and attempted to answer several questions which are still relevant today, in particular:

> *To what extent are the component species of a community mutually selected from a larger species pool so as to "fit" with each other?*
>
> *Does the resulting community resist invasion? If so, how?*
>
> and
>
> *To what extent is the final species composition of a community uniquely specified by the properties of the physical environment, and to what extent does it depend on chance events (e.g. the question of which colonists arrive first, possibly also affecting which subsequent arrivals are compatible with the successful first colonists)?*

Diamond (*op. cit.*) obtained "incidence functions" for the bird species based on observations of their occurrence on islands of different species-richness (S). These functions are fitted curves of incidence of occurrence (proportion of islands of a given richness class occupied, thus taking a value of between 0 and 1) against island richness. So if, for example, a particular bird species was invariably present on islands supporting at least 100 bird species, that species would be given an incidence of 1 for the part of the curve with $S >= 100$. Based on the shape of these functions, the bird species were classified into six types. The incidence functions were then used to estimate the likelihood of different

species combinations on islands of particular richness. Diamond hypothesised that diffuse competition was important in structuring avian communities, and acted as a further constraint on species coexistence above that imposed by habitat requirements etc. He therefore examined whether the predicted likelihood of species' co-occurrence calculated using the incidence functions adequately explained the actual co-occurrences. In some cases, he argued, it did not. In addition to the operation of "incidence rules", he therefore invoked "assembly rules" which are constraints upon species coexistence caused by competitive interactions (rather than just the products of environmental sorting processes). The assembly rules were divided into "compatibility rules" and "combination rules". Compatibility rules were based upon firm ecological knowledge and had an explicit causal component. They might, for example, be based upon observations of species' interactions (e.g. that species *X* can never coexist with species *Y* because *Y* physically interferes with *X* and drives it to extinction under all circumstances). Combination rules were based upon observation (e.g. that species *X* never occurs with *Y*, despite the fact that they have adequate opportunities to do so), but without any knowledge about the reason for this. Diamond's work has proved influential and, it must be added, controversial (e.g. Connor and Simberloff 1979, Diamond and Gilpin 1982, Gotelli and Graves 1996).

Haefner (1981) formulated what he termed the community assembly problem as follows:

> *Construct an algorithm such that, given an arbitrary species pool and an arbitrary collection of environmental factors, the output of the algorithm is a list of species associated with the environment*

His view of community assembly (Haefner 1978 and 1981) is similar in many respects to that of Diamond, incorporating the possibility of forbidden combinations of species resulting from competition, for example. There is, however, a radical difference in the way community assembly is modelled. The generative grammars of theoretical linguistics are used to map a set of species onto a set of environments. To determine the set of co-occurring species, this method involves formulating species insertion rules (including

species in the community list if their requirements - for food, nest sites etc. in the case of bird species - are met by the environment) and then species deletion rules (removing species from the list if they occur in certain 'forbidden' combinations). If community assembly is a complex process, the use of grammars for modelling it has advantages because they can be structured to reflect this complexity. Perhaps the main limitations are the way in which the niche requirements of the species have to be known (a disadvantage when plant species are under consideration), and the binary nature of the predictions. Species are predicted to be present or absent, rather than more or less likely to be present or more or less abundant, a fact that can result in misleading conclusions (Haefner 1981, see also Chapters 3 and 8).

Some recent work into faunal communities of aquatic ecosystems has adopted a simpler view of assembly processes, ignoring the possibilities of forbidden combinations of species and regarding the actual community as resulting from the action of environmental 'filters' on species traits (e.g. Richards *et al.* 1997, Scarsbrook and Townsend 1993). According to this view, species with the right combination of characteristics to live in a particular location pass through the 'filters' created by the environment at that location whilst species lacking the right set of characteristics are filtered out. There is, however, evidence that priority effects of the kind suggested by Diamond (1975) may operate at least on some faunal communities over the short term (Ehmann and MacMahon 1996), and the importance of historical effects on ecological patterns are examined and emphasised by Herrera (1992). A full understanding of community assembly may therefore need to make reference to more than simple filtering processes.

Approaches used to investigate animal assemblages have often differed markedly from those applied to plant communities, although many of the assumptions or basic ideas behind the work are the same. In plant community research there are again the same two processes envisaged (although seldom considered in the same study): community structuring as a result of competition or as a result of environmental influences filtering species on the basis of traits. The main reason for the differences in approach is the way in which, for animals, it is frequently possible to categorise the resource requirements needed

successfully to complete the life cycle. In other words, to a first approximation, their fundamental niche may often be known. Where this is the case, the ecologist can compare the resources required by the species with resources offered by the environment under study, and may be able to rule out some species as community members if their fundamental niche falls outside the range provided by the environment. The possibility that other species may then 'compress' the fundamental niche of potential community members into a smaller realised niche which may or may not be adequate for species persistence can be addressed using, for example, the deletion rules of Haefner (1978 and 1981). The relationship between organism and niche is much more clearly defined for animals than it is for plants, and various authors have actually questioned whether different plant species exhibit niche differentiation (e.g. Silvertown and Law 1987)

Despite the difficulty of identifying plant niches, guilds of plants have been defined, either on an *a priori* basis by the ecologist (e.g. being divided into forbs and graminoids: Wilson and Watkins 1994, or on morphology and life history: Wilson and Gitay 1995), using multivariate statistical methods to cluster the species on the basis of their traits and then using these clusters to define the guilds (Boutin and Keddy 1993, Kindscher and Wells 1995) or as "intrinsic guilds" (Wilson and Roxburgh 1994, Wilson and Whittaker 1995, Wilson *et al.* 1995a). The way the community is structured on the basis of guilds has then been used in an attempt to infer whether competition is an important structuring force in the community and, as a consequence, whether assembly rules are operating. This school of thought (Wilson, 1994) argues that a major programme for vegetation science should be a search for assembly rules (*sensu* Diamond), to see whether they exist, how commonly, where they apply and what rules there are. At present, some significant departures from random assembly have been identified at a small scale on the basis of "guild proportionality" (e.g. Wilson and Watkins 1994, Wilson and Gitay 1995), although other studies have failed to find such evidence (e.g. Wilson *et al.* 1996a) and no predictive rules have yet been offered.

The other line of empirical investigation into plant community assembly has been to regard the environment as filtering species on the basis of their attributes and therefore removing those which are unsuited to the prevailing conditions. This approach is therefore conceptually identical to that used by some ecologists investigating aquatic faunal communities (e.g. Richards *et al.* 1997). An early attempt along these lines was pursued by van der Valk (1981), who produced a qualitative model of wetland succession based on three key life history traits. These, in combination, created 12 basic life history types which were filtered by the physical environment, leading to predictable community composition. This approach has more recently been used by Keddy and co-workers (e.g. Weiher and Keddy 1995a). In this context, the non-randomness in community composition resulting from the filtering effect of the environment upon traits has been termed an "assembly rule" (e.g. Keddy 1992). It is worth noting that this use of the term assembly rule is at variance with that originally intended by Diamond and argued for by Wilson *et al.* (1996b).

1.5 The need for an attribute-based science

To be a predictive science rather than just a descriptive catalogue of special cases, the study of community assembly must be based in some way upon the attributes of the species under study (or an ecological classification of organisms) in order to bypass "the infinite variety of species and populations" (Grime *et al.* 1997a). Such classifications or attributes include guild membership (e.g. Wilson and Watkins 1994), functional groups (Fox and Brown 1995, Fox and Brown 1993, Gitay and Noble 1997, Westoby and Leishman 1997) and life history attributes and other traits (e.g. Leishman and Westoby 1992, Thompson *et al.* 1996, Richards *et al.* 1997). In this way, one may hope to identify the species types (e.g. Noble and Slatyer 1980) which tend to coexist under certain conditions and therefore be able to make predictions about individual species or groups of species based on a knowledge of their attributes.

1.6 Some key issues in community assembly

1.6.1 Conflicting processes

There is a need to clarify the way in which the two apparently conflicting processes described above (section 1.3) operate upon species to form a community. Is there evidence that both processes are at work? This is of importance when one wishes to model community assembly, since a model built upon a sound knowledge of ecological processes is likely to both yield more general predictions and, in turn, to further ecological understanding (e.g. Noble 1987).

1.6.2 Phylogeny

In section 1.5 I have argued for an attribute-based approach to community assembly: one that requires comparisons to be made between species' traits or characteristics and relates these differences to community composition. In recent years (e.g. Harvey and Pagel 1991) it has become clear that comparative studies such as those advocated here should take due account of the evolutionary relationships between the study species. Closely related species tend to be similar in many respects, and two closely related species may, for example, both perform well in a community for reasons other than the traits under study. Phylogenetic methods have been developed to disentangle at least some of the spurious correlations which may arise in studies such as these, and have great potential in community ecology. To date, however, few researchers have used these methods to investigate questions about ecological communities.

1.6.3 Assembly from the species pool

To investigate the assembly of any particular community simply by studying the species which are found in it is to read only the sequel to an unknown story. The community we

see at a particular location and under certain environmental conditions is what might be termed the 'realised community', one particular combination of species out of potentially very many. If we are only interested in this particular community then possible alternative outcomes may be a subject of little interest. If, however, we wish to predict future community composition under certain specified conditions we are no longer dealing with realised communities but potential ones. The way in which a realised community may be assembled from a pool of possible inhabitants then becomes of fundamental importance, a matter which is pursued in various ways in this thesis.

1.6.4 Modelling approach

There is a need to identify an appropriately structured approach to modelling community assembly. The brief review (section 1.4) given above mentions some different types of models, but these in no way exhaust the possibilities which range from the simplest of linear models to the expert systems advocated by Noble (1987). Identification of the different types of processes which may govern community assembly and the stages in the process of community organisation at which they operate is likely to facilitate the selection of the most appropriate models.

1.7 The structure of this thesis

In this thesis I examine some facets of the issues raised above. I investigate the assembly of a grassland plant community from the local species pool, and subsequent smaller-scale processes including some of the effects that different grazing regimes may have upon the plant community. In Chapter 2, I offer a description of the field site which forms the basis for the studies described here. Chapter 3 describes a trait-based investigation of the assembly of the study community from the local species pool and examines the role of the conflicting ecological processes described above. Wherever possible, I use recently developed phylogenetic methods to allow for the degree of relatedness between species

before their traits are examined. Chapters 4 and 5 describe experimental studies of some potential barriers to species colonisation, and again use a phylogenetically corrected method applied to members of the species pool. The experimental studies are relevant both to assembly from the species pool and subsequent more local processes. In Chapter 6 I report the results of wider field investigations into the ecology of the species used in the previous two chapters. Here I attempt to discover more about the niches occupied by the study species and to relate this to the experimental findings. Chapter 7 describes the results of two comparative greenhouse experiments into the effects of defoliation and nutrient regime on two plant species, and has a bearing on plant traits and their relation to plant performance in different environments. In Chapter 8, the themes of the previous chapters are drawn together and discussed. A biological flora for *Cirsium eriophorum*, one of the species used in my study, is given at Appendix 1. The species pool for the study site is given at Appendix 2.

Chapter 2. The Little Wittenham grazing trial

2.1 Site history and general details

Most fieldwork described in this thesis was undertaken within the grazing trial at Little Wittenham Nature Reserve, Oxfordshire (Grid reference SU568924). The reserve is owned by the Northmoor Trust, a charitable trust whose aims and objectives are given in Treweek (1990). The grazing experiment was set up in 1986, with the objective of investigating "....the role of sheep production in the management of areas where the nature conservation value of the grazed sward is of interest" (Treweek *op. cit.*). After arable use during World War II, the site now occupied by the grazing trial was reseeded with a perennial rye-grass/Timothy/cock's-foot mixture and grazed by sheep and cattle. It has been treated in a similar way to most grasslands across lowland England, with fertiliser application being continued until 1982 when the land was purchased by the Northmoor Trust. Since that time, no artificial fertiliser has been applied. The soils of the site are clay loams over a calcareous substrate with a mean pH of 7.5 and a high residual fertility (Watt *et al.* 1996).

Summer 3cm

Treatment	Winter	Spring
A	-	-
B	-	+
C	+	-
D	+	+

Summer 9 cm

Treatment	Winter	Spring
E	-	-
F	-	+
G	+	-
H	+	+

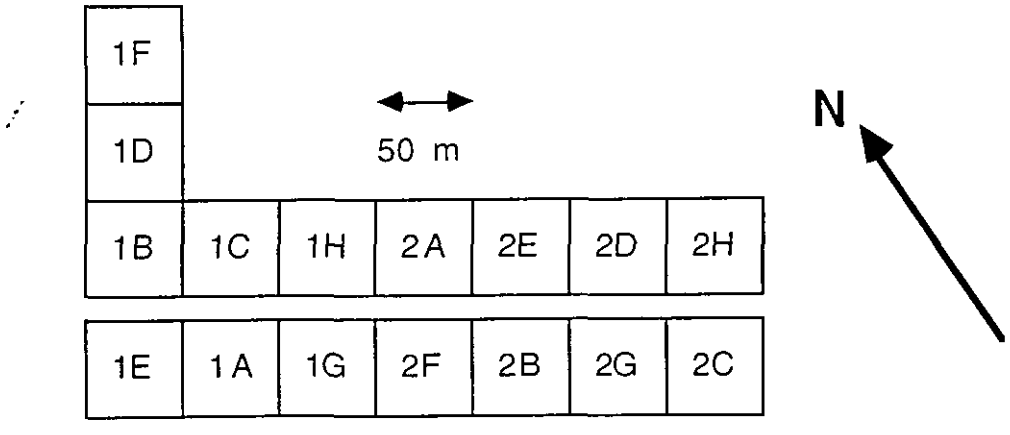


Figure 2.1. The experimental grazing treatments and arrangement of the grazing trial at Little Wittenham.

2.2 Design of the grazing experiment

The experiment comprises a factorial design consisting of 16 paddocks measuring 50 x 50 m each, and organised into two blocks of eight on a randomised basis (Figure 2.1), with three 'seasons' of grazing being applied:

WINTER: NOVEMBER 1 to MARCH 20

SPRING: MARCH 21 to MAY 20

SUMMER: MAY 21 to OCTOBER 31

At each season, grazing is applied at one of two levels. During winter and spring, the levels are *i)* high (+): grazed by two sheep, and *ii)* low (-): not grazed. During the summer the two levels are *i)* high: grazed to 3cm average sward height and *ii)* low: grazed to 9cm average sward height. The sward heights are monitored on approximately a weekly basis during the summer. The grazing treatments are applied in all combinations, with each combination being replicated twice. During the winter and spring grazing periods each paddock has either two sheep or none, according to the treatment imposed. During the summer grazing season, however, the level of sheep grazing within individual paddocks may vary substantially from week to week according to the growth rate of the sward. At some periods during the summer, sheep may be completely absent from some paddocks if the sward height is at or below target level. This is more often the case in the 9 cm grazing treatment, and at the onset of the summer grazing period, paddocks experiencing spring

grazing but low summer grazing may have no sheep on them for a few weeks before the sward reaches the 9 cm target.

2.3 Initial investigations: quadrat survey and species list

Although the grazing trial has been studied for more than a decade (e.g. Silvertown and Smith 1989, Treweek 1990, Silvertown *et al.* 1992, Watt *et al.* 1996, Treweek *et al.* 1997), I considered it important to undertake a baseline study at the start of my project. The main reason for this was the possibility that some of the species formerly recorded from the trial may have become extinct or new ones colonised, and it was important to have an up-to-date species list for the species pool studies. The baseline investigation took the form of a quadrat survey and compilation of a species list for each paddock.

Previous studies show that the different grazing treatments have led to significant differences in the sward between paddocks, creating differences in species richness and affecting species differently according to their identity (e.g. Watt *et al.* 1996). At the level of detail recognised by the National Vegetation Classification (NVC - Rodwell 1992), however, all paddocks are similar, approximating to the MG6/MG7 communities.

In the quadrat survey, 5 quadrats measuring 2 x 2 m were randomly located in each of the 16 paddocks, ignoring a 10 m buffer around the edge of each paddock to minimise 'edge effects'. Compared with similar data for the MG6 and MG7 communities in Rodwell (1992) the plots are of average species richness (Table 2.1), although they fall far short of the richness expected for the more diverse basic grasslands in southern England.

Treatment	**Mean number of species per quadrat (and standard deviation)**	
	Block 1	Block 2
A	9.2 (3.03)	9.2 (1.92)
B	7.6 (1.52)	10.2 (1.30)
C	10.6 (1.14)	12.8 (1.64)
D	12.8 (0.45)	12.4 (1.14)
E	6.2 (0.84)	7.0 (1.13)
F	11.4 (2.51)	10.6 (1.34)
G	12.6 (1.14)	10.6 (1.52)
H	15.2 (0.84)	11.6 (1.14)

Table 2.1. Summary of the 1995 quadrat survey: mean number of species (and one standard deviation in brackets) per quadrat under the different grazing treatments.

An initial study of the paddocks revealed that many species (particularly dicots) occurred as isolated individuals or in very scattered groups in the paddocks. During 1995 I therefore surveyed and recorded the vascular plant species across the full area of each paddock. The list for each paddock soon reached a ceiling of between 17 and 32 species. The species present in the grazing trial are shown at Appendix 2 in bold type.

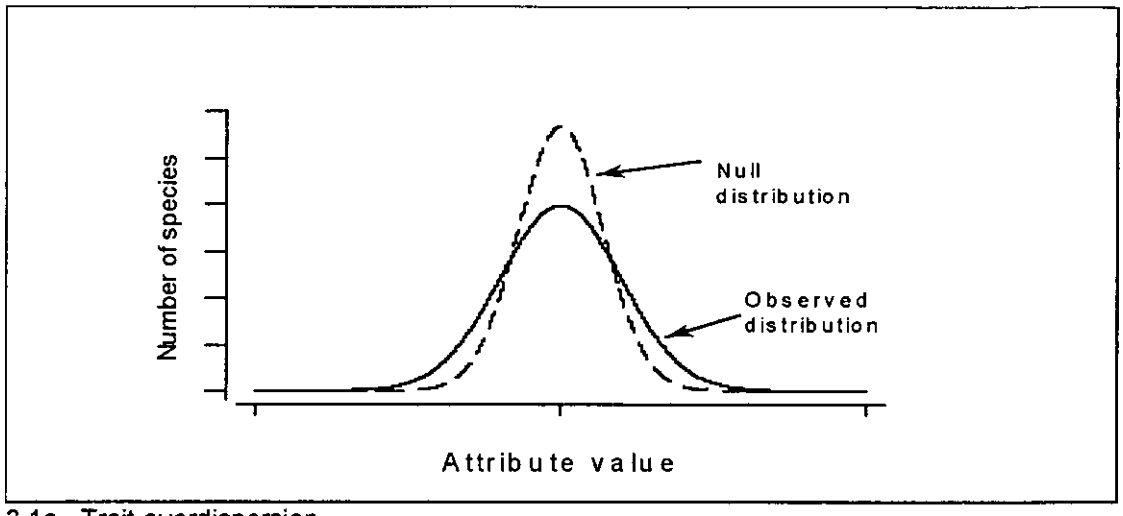
Chapter 3. The assembly of a grassland plant community from the local species pool

3.1 Introduction

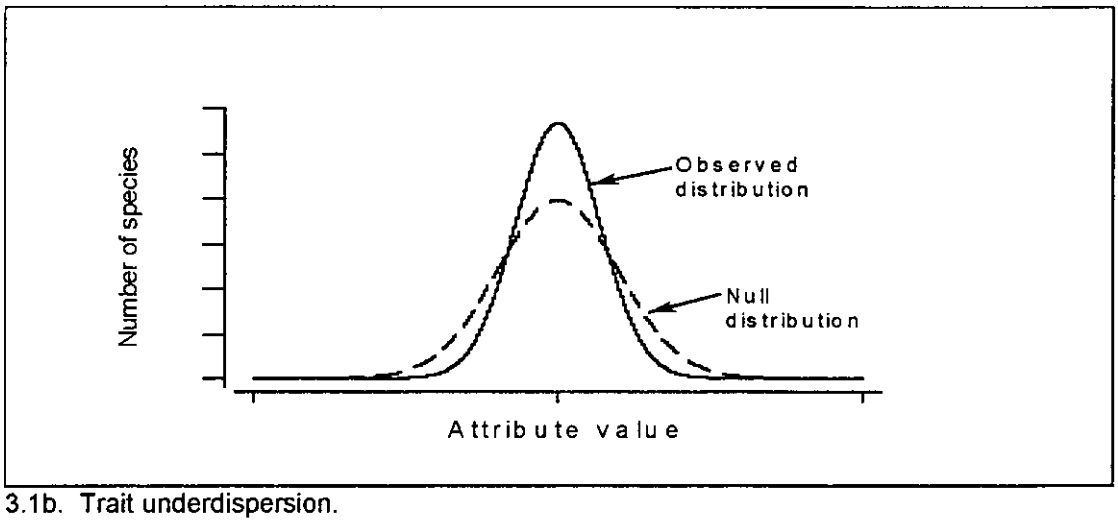
In this chapter I report a study of the assembly of the grassland plant community described in Chapter 2. As argued in Chapter 1, the claim that communities are non-randomly organised is uncontroversial. The interest and difficulty in considering community organisation arise when one asks the following questions: *i)* with respect to what is the community non-randomly organised?, *ii)* how is this non-randomness manifested?, and *iii)* how can the non-randomness be used for prediction of community composition? As previously discussed (section 1.3), there are two schools of thought in ecology leading to quite different expectations about the type of non-randomness to be observed in community assembly. I explore these contrasting predictions using a trait-based approach.

Trait distribution

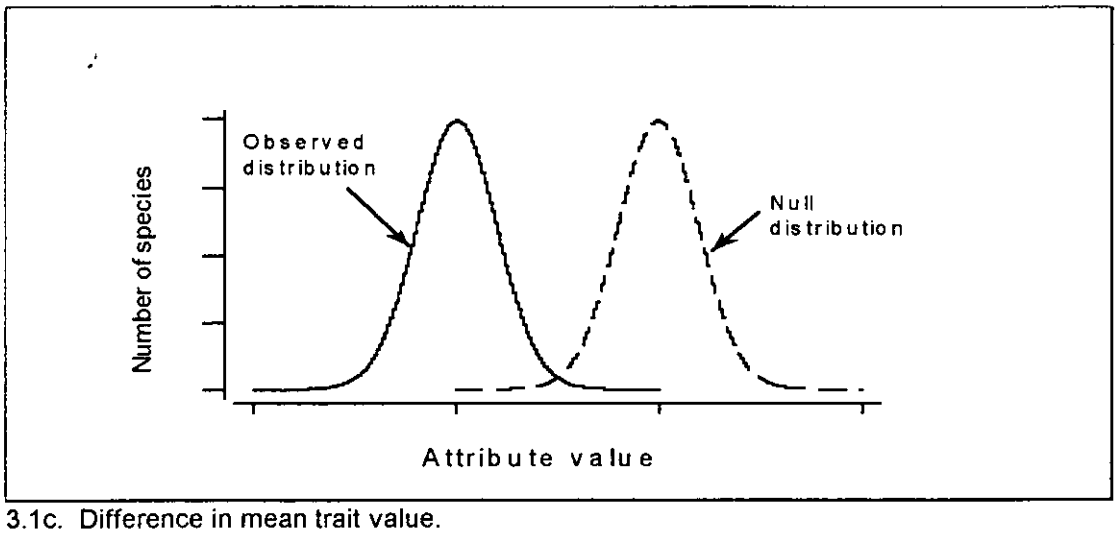
Three types of departure from random trait distribution within communities are illustrated (in the form of a smoothed histogram) in Figure 3.1 with reference to the kind of situation addressed in this chapter. Attribute value is shown along the *x*-axis, and might, for example, represent mean seed weight for each of the n species recorded from the local pool. The *y*-axis records the number of species (total = m, where $m <= n$) within a particular community having a given attribute value. The 'observed distribution' illustrates the range and frequency of trait values for the actual m species within the community, whilst the 'null distribution' illustrates the range and distribution of traits for m species drawn at random from the species pool (see section 3.5 for a discussion of null models).



3.1a. Trait overdispersion.



3.1b. Trait underdispersion.



3.1c. Difference in mean trait value.

Figure 3.1. Three departures from random expectation in community assembly. In 3.1a, trait overdispersion is shown. This has been predicted for traits related to competition. In 3.1b, trait underdispersion is shown. This has been predicted for traits related to overcoming environmental adversity. In 3.1c, a difference in mean trait value is shown, with the set of species in the community having a smaller mean trait value than expected. See text for further explanation.

Figure 3.1a shows trait overdispersion in which a broader than expected spread of trait values is seen. This, it has been argued (Weiher and Keddy 1995b, see also Chapter 1), may be seen if the trait under investigation is correlated with the competitive ability of species. Figure 3.1b shows trait underdispersion. Such a pattern might be observed in traits involved in overcoming environmental adversity (Weiher and Keddy *op. cit.* and Chapter 1). Figure 3.1c shows a difference in mean trait value between the actual and null distributions. This pattern was not discussed by Weiher and Keddy but might emerge if there is selection for trait values of a particular magnitude, for example low-growing plants being favoured in a situation where grazing intensity is high. Differences in mean trait value may of course be combined with differences in trait dispersion to form a 'hybrid' between the situations shown in Figures 3.1a or 3.1b and that of Figure 3.1c.

Species pool and probability of occurrence

I define the species pool of a community as comprising those species which have a non-zero probability of maintaining viable populations in that community (see section 3.2.2.1 for a fuller discussion). It seems reasonable that, of all the species which *might* coexist in a community, some are more likely to be present than others, perhaps because their propagules are more likely to arrive at the site or that they are better suited to conditions there. Law and Morton (1996) argue that "at the very least a probability of arrival per unit time [in a particular community] should be attached to each species [in the species pool]". The importance of a probabalistic interpretation of the species pool has, however, often been overlooked or ignored, with investigators assuming, tacitly or not, that species in the species pool have an equal likelihood of establishment in the community (e.g. Haefner 1981, Eriksson 1993). In view of this, after investigating whether the species in the study community are a random sample from the species pool with regard to selected traits, I then investigate whether it is possible to use these traits to estimate the probability of occurrence and rank abundance of species in the community.

3.2 Methods

3.2.1 The study site and general approach

The site used to examine these ideas is the experimental grazing trial at Little Wittenham described in Chapter 2. For the purposes of the work in this chapter, no account has been taken of the differences within the grazing trial due to different grazing regimes. The grazing trial is therefore treated as a homogeneous unit. The primary reason for this is that there are few species restricted to only one combination of grazing regimes, and the sample size is therefore insufficient to detect any differences in plant traits between treatments if the study is based on species presence/absence as it is here. As explained in Chapter 2, the different grazing combinations have led to significant differences in the abundance of some species (and species richness), but at the level of resolution normally adopted for community classification (e.g. Rodwell 1992), the paddocks are all similar. This study examines forbs only, and all graminoids (grasses and sedges) are therefore excluded. There are three reasons for this. First, and most importantly, there is little to distinguish many of the graminoids from one another in terms of the traits recorded in section 3.2.3, whereas the forbs comprise a diverse set of species. I therefore concentrate attention on the forbs because this is the group most amenable to study. Secondly, the site is grass dominated and there is therefore an interest in discovering more about why the forbs are scarce. If answers to this question are found, steps can be taken to increase the diversity of the site. Thirdly, there is a possibility that species in two groups (forbs and graminoids) may be assembled into communities according to different rules. In an attempt to identify the important traits affecting community assembly, the chance of success will probably be greater if the groups are examined separately

3.2.2 The species pool

3.2.2.1 What is meant by the term 'species pool'?

The term species pool has been variously understood. In some cases, it has been used simply to mean all the species (or species of a particular kind, such as vascular plants) that there are in a given area (e.g. Poff 1977). Such use of the term is inadequate in community ecology, because it takes no account of whether the species in the species pool have even the most remote chance of growing in the community (or communities, see section 3.2.2.2) of interest (cf. Zobel 1997). If one followed this usage, many pondweed (*Potamogeton*) species would be members of the chalk grassland species pool in southern England! I define the species pool as comprising those species which have (or are believed to have, on the best available evidence) a non-zero probability of maintaining viable populations in the study community/communities (where communities are defined, as far as is possible, on the basis of environmental data rather than the vegetation itself, cf. Eriksson 1993). Within this definition I further subdivide the species pool into the regional pool (those species present anywhere within the British Isles meeting the above criterion) and the local pool, a subset of the regional pool restricted (for reasons of convenience described in section 3.2.2.2 below) to those species occurring in the 50 x 50 km square centred on the grazing trial. All species in the regional pool which are absent from the local pool are assumed unable to colonise the site due to dispersal limitation. Even within the local pool, however, dispersal limitation may operate (e.g. Primack and Miao 1992). This possibility is investigated here. My definition of the species pool could further be strengthened by attaching a temporal dimension to it. Species in communities may come and go for a whole host of reasons including environmental stochasticity, and one might well ask 'for how long does a species have to be able to "maintain" viable populations in order to be considered a potential community member?' I omit any reference to time from my definition simply because adequate information is not available to implement it.

3.2.2.2 Selection of the species pool

The British flora comprises more than 3500 vascular plant species (Kent 1992, Kent 1996), this list thus forming an upper limit to any British species pool. It is clear, however, that not all species can be expected to occur in grassland, and even considering grassland species alone, not all will occur under the environmental conditions prevailing at Little Wittenham. Experimental delimitation of the species pool although ideal in theory is clearly impracticable. Given sufficient data about the plants and their ecological tolerances and requirements, an alternative approach would be first to circumscribe the regional species pool by defining a multivariate habitat 'space' based upon the situation prevailing at the site, and then to select those species having niches which fall within this space. An approach along these lines was followed by Pärtel *et al.* (1996) using the Ellenberg numbers (Ellenberg *et al.* 1991) for light, soil moisture, pH and nitrogen content to define the axes of the habitat space. I tried adopting a similar approach, but found the Ellenberg numbers to be a crude means of selecting species. To take an example, the N (soil nitrogen) number can take integer values from 1 to 9, but the species currently present in the grazing trial span most of this scale (ranging from 3 to 8). A similar situation prevails with regard to the other Ellenberg numbers (see also Hawkes *et al.* 1997), and a selection criterion based upon them was caught upon the horns of the following dilemma. A broad range of Ellenberg numbers must be adopted to avoid the absurdity of having species in the grazing trial which are absent from the species pool. Broadening the range sufficiently, however, results in most of the British flora being accepted, including many species that no competent botanist would ever imagine taking root at the site.

Instead, the NVC (Rodwell 1992) was used as a means of circumscribing the species pool. The grazing experiment is situated on basic soils (pH circa 7.5) which are relatively deep and fertile, and the approach I have followed has been to ignore NVC grassland communities for which the conditions at the site are clearly unsuitable. From the remaining communities, the regional species pool has been drawn up from the separate NVC lists,

subject to the additional procedures described below. Most species listed in the species pool are represented in several of the selected NVC communities, so the species pool defined here seems to be a relatively robust construction. All aspects of the environment at the grazing trial (e.g. soil type, altitude, soil moisture regime etc.) mentioned in the NVC community descriptions were taken into account, *except* for details of the management regime, since the effects of the current grazing regimes were to be investigated as a part of this study (see section 3.2.3.3). This highlights an important additional matter concerning the delimitation of the species pool. The way it should be drawn up is determined in part by the nature of the question posed by the investigator. If I were simply interested in the species which might grow in the grazing trial as it is managed today, the species pool would be smaller than the one I eventually selected. The species pool listed in Appendix 2 therefore contains some species which may be unsuited to current conditions at the site, but may be able to grow there under altered management. The only management constraint I have applied here is that it must be such that the site remains a grassland.

The following grassland community lists 'contributed' species to the species pool: MG1, MG5, MG6, MG7, CG3, CG4, CG5, and CG6. In a very few cases, species were omitted because they occurred in a particular subcommunity or variant characterised by a different environment from that of the typical community; for example *Iris pseudacorus* is characteristic of a winter flooding river-valley variant of MG6a, and was consequently omitted from the list. Since the species lists in Rodwell (1992) exclude plants which occur but rarely in the NVC communities, some species which are infrequently encountered in mesotrophic and calcareous grasslands are absent from the list described above. To eliminate this problem, habitat descriptions were studied for all species in Clapham *et al.* (1987), and any additional species of lowland mesotrophic and calcareous grasslands absent from the above list were added. The eventual list of species comprises the regional species pool. It includes a few species (such as *Phyteuma orbiculare*) which, although growing in basic grasslands in southern Britain, are local and do not occur near the study site. Such species are almost certain to be dispersal limited (even if no other barriers to colonisation were to operate if propagules arrived at the site), and burdening the data set with taxa

having effectively a zero probability of occurrence is likely to obscure rather than clarify the relationship between the traits of the species and their presence in or absence from the study community. For this reason, a local species pool was defined, comprising only species recorded from the 50 x 50 km square centred on the grazing trial. Ideally, a smaller area might be preferred from which to define the local species pool. In the present case, however, some species known to occur within the 10km square in which the grazing trial is situated are shown in Perring and Walters (1962) as absent. This is likely to be an artefact of under-recording, and the larger 50 x 50 km square was considered to be a satisfactory compromise which avoids the effects of under-recording whilst still retaining the 'local' character of the species pool. The local species pool is listed in Appendix 2.

Note that all members of the species pool are not considered equally likely to be members of the study community (cf. Pärtel *et al.* 1996). Indeed, it is inevitable that there will be differences in their probability of occurrence which is also likely to be reflected in their abundance in the community. This will be the case no matter how the species pool is derived: some species will be rare in or absent from the target community whilst others will be widespread, perhaps due to differences in dispersal ability, fine differences in edaphic requirements etc. It is just such differences, however, which are the subject of scrutiny in this chapter, and the implications of the probabalistic nature of the species pool are taken up in Chapter 8.

3.2.3 The trait matrix

Data collection was restricted to published sources. Some traits (such as life form) were omitted from the data matrix after initial consideration, because there were too few contrasts in the data set to make a useful comparison. Eventually, 10 attributes were identified and scored or quantified as explained below. Since the data were taken from a number of sources, not all species have data for all characters. The data have been treated as either binary or continuous variables, although some of them are not, strictly speaking,

continuous but ordinal. Due to the use of randomisation tests in this study (see Sections 3.3.2 and 3.3.3 below), however, this does not affect the validity of the analysis. For simplicity, all the variables recorded here are in places referred to as 'traits', although the abundance of species in a particular area is clearly not a trait in the proper sense of the word.

3.2.3.1 Competitive ability (COMP)

Grime (1977) argues for the existence of three primary strategies in plants, and a classification based on the strategy (or combination of strategies) they adopt is given in Grime *et al.* (1988). At the extremes, plants may be competitors (C), ruderals (R) or stress tolerators (S), although many species adopt an intermediate strategy such as CR or CSR. Given that the grazing trial has been out of commercial agricultural use for only fifteen years, one might expect the species present to be the stronger competitors that are typical of agricultural situations. It is possible to convert the competitiveness of a plant in the scheme of Grime *et al* (*op. cit.*) to a numerical value, and that procedure was adopted here. Plants which are wholly competitors, ruderals or stress tolerators were given a score of 12 for the strategy they adopt, and zero for the others. Plants exhibiting intermediate strategies were given intermediate values as appropriate. Thus a CR plant would be given a C-value of 6, an R-value of 6 and an S value of zero. In this way it is possible to record three strategy scores for each plant, whatever strategy combination it exhibits, and the total score will always sum to 12. Competitive ability was quantified as the C value described above.

3.2.3.2 Nutrient level (NUTR)

The grazing trial is a relatively nutrient rich site (Chapter 2), and there is therefore reason to suppose that those species in the local pool which can tolerate (or which require) higher levels of nutrients will be favoured (cf. McKendrick 1996). Plants may respond differently to nutrients of different kinds, but quantitative data on the responses of most

species to different nutrients are lacking. The only appropriate source of data which could be found was the Ellenberg N (nitrogen) value (Ellenberg *et al.* 1991). Despite being derived from observations on the Central European flora, these numbers have proved useful predictors of plant requirements/tolerances in Britain (Thompson *et al.* 1993). Although the Ellenberg N value was found to be unsuitable for partially *defining* members of the species pool, it may still be adequate to identify significant differences between two subsets of a species pool defined by other means.

3.2.3.3 Flowering period (TOTFLO and FLO)

During the summer months (June to October) the sward height at the grazing trial is kept at a pre-determined level (either 3cm or 9cm) and sheep are added or removed as required. Staff at the nature reserve have suspected that grazing during the summer months may act as a barrier to species diversity, and initial studies (R. Tofts, unpublished data) suggest that close grazing during the flowering period leads to a reduction in species richness. Examination of the relationship between grazing and flowering period is therefore of value in identifying suitable grazing regimes for conservation management. It is worth stressing that, for the species which occur in the grazing trial, there is already strong evidence that excessive summer grazing can have an adverse effect on species performance (e.g. Bullock *et al.* 1995, Watt *et al.* 1996, R. Tofts, unpublished data). What is not known is the extent to which the current grazing regimes prevent some species from occurring in the grazing trial at all. Data on the flowering period were taken from Clapham *et al.* (1987). Two variables (in months) were recorded: *i)* the total length of the flowering season (TOTFLO), and *ii)* the length of the flowering season outside the summer grazing period June to October inclusive (FLO). Based on the assumption that recruitment from seed is important, the expectation is that forbs with a longer flowering period or which flower for a greater length of time outside the summer grazing period will be favoured, because they are the ones which will be more likely to flower and set seed without being grazed off.

3.2.3.4 Plant height (MINHT and MAXHT)

It has been suggested (e.g. Mitchley 1988) that grassland plants may experience a trade-off between *i)* growing tall and maximising the amount of light they are able to intercept, and *ii)* maintaining low growth to minimise the amount of biomass lost due to grazing or mowing. Since sheep grazing to a sward height of 3 cm or 9 cm occurs during the period in which most plants are growing steadily, there is reason to suppose that plant height may be an important factor in determining presence or absence from the grazing trial, with the expectation being that shorter plants will be favoured. Data were obtained from Clapham *et al.* (1987), and where data were lacking, Stace (1991). Lower (MINHT) and upper (MAXHT) height values were both recorded (in cm).

3.2.3.5 Dispersal mechanism (DISP)

Seed dispersal is an important factor in determining which species colonise a particular area even at a local scale of tens or hundreds of metres (e.g. Bakker 1989; Eriksson and Ehrlén 1992; Primack and Miao 1992). This may be particularly evident in cases where an area has not long been available for colonisation. One would expect that the species with better powers of dispersal will be those that are favoured in the grazing trial. Dispersal information was taken from Grime *et al.* (1988). Following Thompson and Hodgson (1996), species in the data set were simply classed as having either good or poor powers of dispersal. Initially, two lists were compiled, a liberal list treating doubtful structures such as awns as dispersal adaptations, and a conservative list which did not. In the event, the conservative list yielded too few comparisons to be of use, and only the liberal list was used in the analysis.

3.2.3.6 Seed weight (SDWT)

Large seed size might be expected to confer benefits upon plant species in certain environments. Larger seeds will tend to have greater quantities of resources for initial seedling establishment, and where the environment of the seedling is particularly harsh, larger seeded species may have the advantage. They may benefit either by enjoying a competitive advantage, or by being better able to cope with temporary carbon deficit during the early stages of growth (Armstrong and Westoby 1993, Leishman and Westoby 1994a, Osunkoya *et al.* 1994 and Saverimuttu and Westoby 1996). Any seedling emerging in the grazing trial is likely to face a high-competition environment, and large-seeded species may therefore be favoured (cf. Burke and Grime 1996). Seed weight data were taken from Grime *et al.* (1988).

3.2.3.7 Vegetative means of reproduction (VEG)

Given that the sward is relatively closed and grass dominated, opportunities for vegetative reproduction may exceed those for reproduction by seed. If this is the case, a disproportionately large number of vegetative reproducers may be present. The presence or absence of vegetative means of reproduction was taken from Grime *et al.* (1988).

3.2.3.8 Longevity (ANN and LONGV)

In an established grassland on relatively nutrient rich soils such as the grazing trial, one might expect the sward to be dominated by longer-lived perennial species. Longevity was assessed in two ways. In the first, plants were classed as annuals or not on the basis of information in Clapham *et al.* (1987). In the second, an 'index' of longevity was calculated following the scoring system of Rees (1996). This quantifies longevity by scoring 1 for annuals, 2 for biennials, 3 for monocarpic plants and 5 for perennials. Plants in composite categories are given a weighted score with the first term being given a weight of 1 and

the second 0.5. Thus a species listed as annual/perennial would be given a score of (1+(0.5 x 5))/(1+0.5)=2.33.

3.2.3.9 Abundance (ABUND)

It is inevitable that there will be differences in abundance between plant species in the species pool. All other things being equal, one would naturally expect abundant species to be more likely to occur in the paddocks than rare species or ones restricted in their distribution. I was unable to obtain data which explicitly measure abundance, but data on plant distribution in the form of dot maps are available and these data were used instead. It is generally accepted that such maps provide an estimate of species frequency (Rich and Smith 1996), and this estimate will improve as the scale of recording becomes finer. Data on the extent of plant distribution were taken from Perring and Walters (1962). More recent maps are available for some species, but these are mainly for rarer species and were ignored since this would have introduced undue bias into the data. For the purposes of this study, the use of old maps is unlikely to be a serious disadvantage, because such changes as there have been over the intervening period are likely to have increased the difference in abundance between the rarer and more common species. The test as performed here will therefore tend to be a conservative one. A more extensive grid than the 50 x 50 km square used for determining the local species pool was required, in order to obtain a sufficiently sensitive measure of abundance. The number of 10km squares occupied within a 110 x 110 km square centred on the grazing trial was therefore taken to provide an indication of abundance.

3.2.3.10 Seed bank (SDBNK)

Data on the seed bank were taken from Hodgson *et al.* (1995). In this case, there was no prior expectation of a particular result. It has, however, been shown in at least one grassland community (Thompson *et al.* 1996) that the species may be organised along the regeneration niche (Grubb 1977), and seed bank properties may therefore be important in the community under study here.

3.3 Data analysis

For this study it is desirable to take account of phylogeny (see e.g. Harvey & Pagel 1991, Kelly 1996). Using seed size as an example to illustrate why, consider the following hypothesis: 'small seeded forbs are absent from the grazing trial because the seedlings are not able to draw upon sufficient reserves to overcome competition by the dominant grasses'. Members of the Orchidaceae are completely absent from the grazing trial, and they also have tiny 'dust' seeds. Should each absent orchid be taken as independent support of the hypothesis stated above? In this case, the answer must be no. Not only do the orchid species have small seeds, but they also share many other characteristics (e.g. the need for a mycorrhizal symbiont, geophytic life form etc.) and they can not be regarded as independent samples in the hypothesis test. Ideally, a test should take account of this lack of independence between species and some such methods are now available. I investigate the distribution of trait values (section 3.3.1) using the method of phylogenetically independent contrasts which makes allowance for the degree of relatedness between species (see Harvey and Pagel 1991), but investigate trait under- and overdispersion (section 3.3.2) using randomisation tests which do not correct for phylogeny. In cases where underdispersion is linked to differences in trait magnitude (see sections 3.1 and 3.5), however, ignoring phylogeny is less problematic provided it has been taken into account where the differences in magnitude are concerned. The discriminant analysis study

(section 3.3.3) also does not incorporate phylogenetic information, although the selection of predictors was restricted to those identified from the phylogenetically corrected part of the study.

3.3.1 Analysis of trait values

Phylogenetic methods have seldom been used in community ecology (but see Losos 1996), although Ackerly and Donoghue (1995) argue that their use in this context is potentially of great value. In order to use phylogenetic methods, one must first construct a phylogeny giving the conjectured relationships between the species being studied.

The overall structure of the phylogenetic tree was taken from Chase *et al.* (1993). For the lower-level details, the following works were consulted: Bremer (1994), Caputo and Cozzolino (1994), Chappill (1995), Downie and Katz-Downie (1996), Doyle (1995), Hsiao *et al.* (1995), Jansen *et al.* (1990), Pillay and Hilu (1995), Plunkett *et al.* (1995), Plunkett *et al.* (1996), Susanna *et al.* (1995) and Wagstaff *et al.* (1995). In cases where a phylogeny was unavailable, a taxonomic structure was used. The primary sources of taxonomic reference were Stace (1991) and Mabberley (1990). The phylogenetic tree thus derived provided the "working phylogeny" which was used in the analyses described below.

Analysis of binary variables follows the method of Read and Nee (1995), with statistical significance being assessed using the sign test. Contrasts for continuous variables were obtained using the method of independent contrasts (Felsenstein 1985) implemented by the CAIC computer package (Purvis and Rambaut 1995). The matter of testing for statistical significance for the continuous variables presents two important problems:

i) Many of the 'continuous' variables described above really comprise ordinal data. Phylogenetically corrected methods for dealing with such data have, however, not yet been developed.

ii) The local species pool can not be regarded as a random sample of a larger population, but rather it comprises the entire population in the statistical sense of that word. The species present in the grazing trial form approximately one quarter of this population, and thus some allowance needs to be made for the fact that test statistics in their standard form will be biased.

These two problems were solved by means of randomisation tests (Manly 1991). Depending upon the trait in question, the data set contained between 12 and 37 contrasts (see Table 3.1). The randomisation tests took the following form. Two mutually exclusive groups of species (i.e. sampling without replacement) were drawn at random from the full data set, with the number of species in each group being equal to the number of contrasts for the trait under investigation. A *t*-test was performed on the two randomly selected groups, and the value of the *t*-statistic recorded. This process was repeated 10,000 times, and the statistical significance of the actual *t*-value assessed against the randomisations.

I took no account of species abundance in the surrounding landscape when comparing the distribution of trait values between the species present in the grazing trial and those not, and every species therefore had an equal chance of selection in contrast to some other studies (e.g. Richardson *et al.* 1995). This resulted in abundance being treated as a separate variable on an equal footing with traits such as Ellenberg N value. This was in part due to practicability and part to theoretical considerations as discussed in section 3.5.

3.3.2 Analysis of trait over- and underdispersion

To determine whether traits are over- or underdispersed one must examine the ratio of trait variance to a null variance. In the present instance, the variance for a particular trait was calculated for the *s* species within the grazing trial (Var_{within}) for which there were trait data, and then the variance for an equal number of species randomly chosen from the species pool but not occurring in the grazing trial ($Var_{outside}$) was calculated. The ratio

Var_{within} / $Var_{outside}$ indicates whether traits are over- or underdispersed in comparison with the expected value of 1. Statistical significance was determined by randomly selecting two groups of *s* species from the entire species pool (the group members being mutually exclusive), calculating the variance ratio and repeating the process 10,000 times in a similar way to that described in 3.3.1 above. The observed variance ratio was then compared against the null distribution and its statistical significance assessed.

3.3.3 Prediction of species presence/absence and rank abundance

The analyses described in paragraphs 3.3.1 and 3.3.2 are intended to detect non-randomness either in trait magnitude or trait dispersion. If either of these is detected, the matter of using this non-randomness to predict species occurrence or abundance arises. This is discussed further in Chapter 8. For the present, I use discriminant analysis in an attempt to predict which species will be present in the community or not, based upon traits identified using the method of phylogenetically independent contrasts (section 3.3.1). Several methods of discriminant analysis now exist (see e.g. Krzanowski 1988). I employ the original form: the linear discriminant function (Fisher 1936). This method produces a function which is linear in terms of measured attributes (selected traits in this case) and, within this constraint, maximises the ratio between the means of the groups to the standard deviations within groups (Fisher *op. cit.*). The function can be used to assign individuals to groups (where groups are known *a priori*) on the basis of the attributes. For the discriminant analysis performed here, prior probabilities although known were not used. The reason for this is that they will in the general case be unknown, and their omission makes for a more stringent but realistic test. For a discussion of the use of prior probabilities, see Krzanowski (1988). Cross validation (see Krzanowski *op. cit.*) was used in order to obtain a more realistic idea of the efficiency of the function.

It has been argued (Poff 1997) that a probabilistic approach is more likely to give useful guidance as to abundance or occurrence of individual species in a community, rather than

an approach which attempts to yield a simple yes/no answer to species presence. The main problem with reliably predicting species presence/absence is a direct result of the crude binary nature of the task. One individual of an 'atypical' (and mispredicted) species weighs as heavily against such a model as a thousand individuals of a correctly predicted species support it. When a probabalistic approach is adopted such as that advocated in Poff (1997), rather than predicting that a species will be either present or absent, one can say that species *X* has a high or low probability of being present. It is possible then to extend this logic by predicting that those species with the highest probability of occurrence will (if the predictive model is a good one) be those best suited to conditions in the community. They are thus predicted, overall, to be those which are the most abundant members of the community. An approach along these lines treats the species pool as probabalistic (e.g. sections 3.1, 3.2.2.2) with the likelihood of species entering a particular community and their abundance within it varying according to their suitability to the conditions there and the probability of their arrival. In addition to using the results of the discriminant analysis to classify the species into two predicted groups (present or absent) on the basis of their traits, the rank correlation between the *probability* of their occurrence generated by the discriminant function and abundance in the community was examined. A measure of abundance for all species present in the grazing trial was obtained from the 1995 survey described in Chapter 2. The measure of abundance used here was the number of quadrats occupied by a species, and therefore took the form of a number between zero and 80. Those species present in the grazing experiment but not in the quadrats were given a nominal abundance rating of 0.5. The discriminant analysis predictions are further examined by giving particular scrutiny to those species which the model suggests should be present but are not, and vice versa.

3.4 Results

3.4.1 Trait values

From Table 3.1 it can be seen that significant differences are recorded for four variables, namely COMP, NUTR, TOTFLO and ABUND. A marginal result is recorded for FLO. In each of these cases the difference is in the expected direction. The view that the current grazing regimes may have the effect of filtering out potential community members is therefore supported ($0.0001<p<0.001$ for TOTFLO, $0.001<p<0.01$ for FLO, both tests 1-tailed), and the recent agricultural past of the site appears also to have left its mark upon the community, with a preponderance of competitive species ($0.0001<p<0.001$ for COMP, both 1- and 2-tailed) and those which require (or tolerate) a high nutrient level ($0.001<p<0.01$ for NUTR, 1-tailed). As expected, species more abundant in the surrounding countryside are also better represented in the grazing trial ($p<0.0001$ for ABUND, both 1- and 2-tailed).

3.4.2 Under- and overdispersion of traits

Table 3.2 shows the results of the trait dispersion analyses. If one-tailed tests are considered, the dispersion of two variables departs (at least marginally) from random expectation, with less convincing results for a further two variables. In contrast with differences in mean trait value, however, the use of one-tailed tests in assessing the significance of trait dispersion is more problematic because of the conflicting predictions of ecological theory. Significant underdispersion was identified for ABUND ($p<0.0001$, 2-tailed) and a marginal result for NUTR ($0.01<p<0.05$, 2-tailed). Inconclusive results were found for two other traits only if one-tailed tests are considered, with marginal underdispersion in DISP ($0.01<p<0.05$) and marginal overdispersion in vegetative reproduction ($0.01<p<0.05$).

Variable tested	Number of contrasts	In expected direction?	Significance 1-tailed 2-tailed
1) COMP	33	Yes	**p=0.0003** **p=0.0008**
2) NUTR	34	Yes	**p=0.0024** ***p=0.0053***
3a) TOTFLO	23	Yes	**p=0.0007** **p=0.0012**
3b) FLO	23	Yes	***p=0.0074*** ***p=0.0173***
4a) MINHT	37	-	p=0.3495 p=0.7091
4b) MAXHT	37	-	p=0.2250 p=0.4619
5) DISP	15	Yes	p=0.0593 p=0.1186
6) SDWT	32	-	p=0.3183 p=0.6304
7) VEG	27	-	p=0.1238 p=0.2476
8a) ANN	12	-	p=0.1134 p=0.2268
8b) LONGV	37	-	p=0.4794 p=0.9795
9) ABUND	35	Yes	**p=<0.0001** **p=<0.0001**
10) SDBNK	33	N/A	p=0.9463 (2-tailed)

Table 3.1 Summary of trait value analysis. For each of the 10 variables tested, the number of contrasts is shown, followed by a column which indicates (for all results with p<0.1) whether the result was in the direction expected on the basis of theory. The final column shows the probability values. Bonferroni corrected 5% cut-off at p=0.0051.

Variable tested	Variance ratio	Significance 1-tailed 2-tailed
1) COMP	2.041	p=0.0730 p=0.1530
2) NUTR	***0.555***	***p=0.0135*** ***p=0.0275***
3a) TOTFLO	0.473	p=0.2168 p=0.4436
3b) FLO	0.700	p=0.3590 p=0.7184
4a) MINHT	0.694	p=0.1733 p=0.3929
4b) MAXHT	0.950	p=0.4500 p=0.8952
5) DISP	***0.863***	***p=0.0471*** p=0.0945
6) SDWT	0.866	p=0.2473 p=0.4979
7) VEG	***1.200***	***p=0.0320*** p=0.0673
8a) ANN	1.403	p=0.2065 p=0.4153
8b) LONGV	1.133	p=0.3394 p=0.6867
9) ABUND	**0.105**	**p<0.0001** **p<0.0001**
10) SDBNK	0.7892	p=0.1741 p=0.3438

Table 3.2 Summary of trait dispersion analysis. For each of the 10 variables tested, the variance ratio is shown. The null ratio is 1, with overdispersion resulting in a larger ratio, and underdispersion resulting in a smaller one. The third column shows the probability values. Bonferroni corrected 5% cut-off at p=0.0051.

3.4.3 Prediction of species presence/absence and rank abundance

Several significant differences in trait value were detected between the species present in the grazing trial and those not. This provides evidence that the study community is not assembled at random from the local species pool. Following an initial evaluation of the five statistically significant predictors identified in section 3.4.1, the two traits ABUND and TOTFLO were used in a discriminant analysis. Addition of TOTFLO to the model containing ABUND (the single best predictor) improved the predictions of the discriminant analysis, but this improvement was not statistically significant (p>0.05). On balance, I chose to retain TOTFLO in the model because of the weight of independent evidence that grazing during the flowering period adversely affects plant performance. The lack of statistical significance is likely to be in large part a product of the relatively crude way in which TOTFLO was quantified. Table 3.3 summarises the results of this analysis.

Put into group	**True group 0**	**True group 1**
0	70	1
1	45	33
Percentage correct	61%	97%

Table 3.3. Summary of discriminant function classification. The classification scores were calculated as S_0=-5.60202+0.07585ABUND+1.04542TOTFLO and S_1=-9.66530+0.11067ABUND+1.20743TOTFLO. Subscripts denote the two groups (0=absent from grazing trial, 1=present). A species will be placed in the group for which it has the highest score.

Overall, the proportion of correctly classified species was 69%. Thus approximately one third of all species was misclassified. From Table 3.3, it can be seen that the errors in assignment to groups are unbalanced. Species which are actually present in the grazing trial are almost invariably (33 out of 34) predicted to occur there. Where the function fails is in correctly assigning absent species to group 0, with 45 out of 115 species being wrongly placed. The discriminant function therefore predicts a large number of (actually) absent species to be present.

The probabilities of occurrence generated by the discriminant function (hereafter termed 'discriminant probabilities' for convenience) are plotted against abundance in the grazing

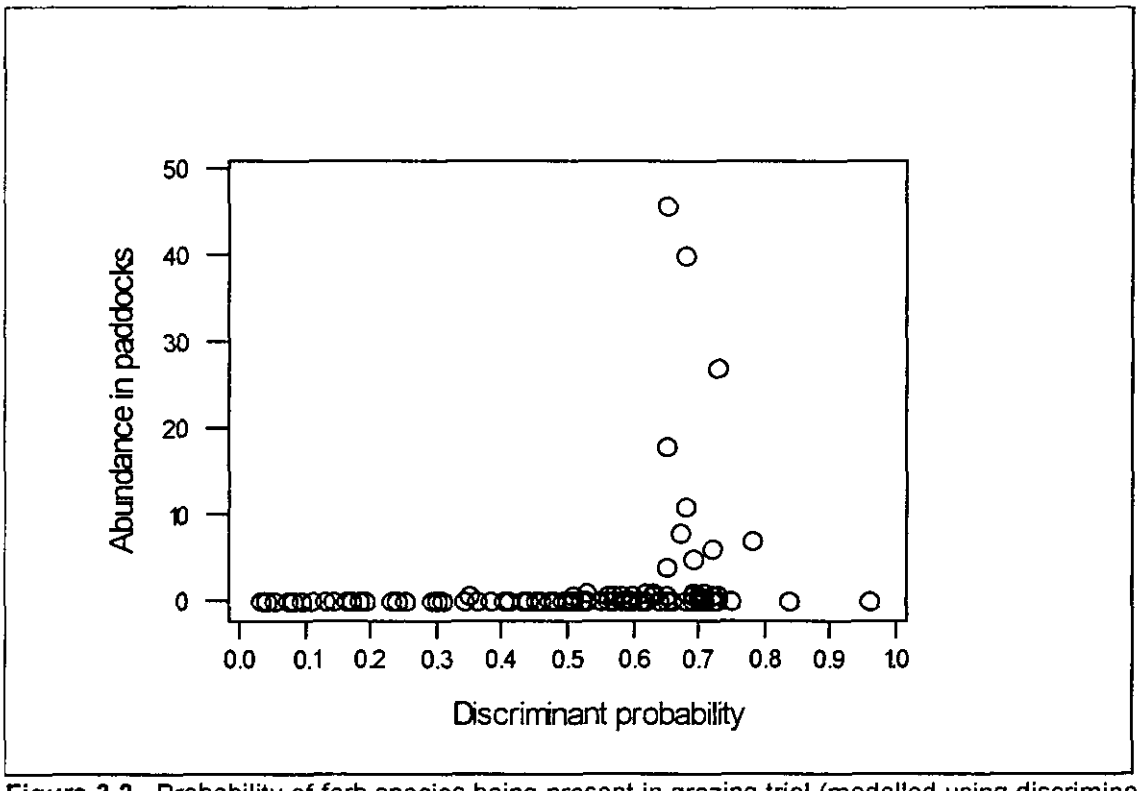


Figure 3.2. Probability of forb species being present in grazing trial (modelled using discriminant function) against abundance of forb species in the grazing trial. See text for further details.

experiment in Figure 3.2. For probability of occurrence and abundance, the rank correlation coefficient r_s=0.495 (n=149, p<<0.0001). There is therefore a statistically very significant relationship between the predicted likelihood of occurrence in the grazing trial and the abundance of the species in it. In particular, species with a low estimated probability of occurrence are indeed either rare or absent from the grazing trial. All except the rarest species in the grazing trial have a discriminant probability of 0.65 or more.

Figure 3.2 is perhaps most instructive, however, when one considers cases in which it fails. I first examine those species with a high discriminant probability (p>= 0.65) but which are absent from the grazing trial. On the basis of field experience gathered over a number of years, I have divided these species into four groups (Table 3.4). This is a relatively crude categorisation, but useful as a first step in trying to discover where the discriminant function fails. Group A species are those that I associate mostly with disturbed or trampled ground. This opinion is supported when the R value (the ruderal score of Grime *et al.* 1988) is

compared for the group A species and all other species with a high (p>=0.65) discriminant probability. The group A species have a significantly (Mann Whitney test, p=0.015, 2-tailed) higher ruderal score than the others. The group B species are those that I associate mainly with taller grassland than that of the study site, such as MG1 communities of the NVC (Rodwell 1992) which often occur on neutral or basic soils under conditions of infrequent mowing. To examine this impression, for each species I recorded the proportion of MG1 to total number of communities it inhabits, taking the information from Rodwell (*op. cit.*). Thus, for example, a plant which is listed only as an MG1 species would be given a value of 1, a plant which is not recorded as an MG1 species would be given a value of zero, and a plant which occurs in the MG1 community plus three other community types would be given a value of 1/(1+3)=0.25. This value therefore gives an indication of the extent to which the species are restricted to the taller MG1 types of grassland. When the group B species were compared against all other species with a high (p>=0.65) discriminant probability, they were found to be significantly (Mann Whitney test, p=0.002, 2-tailed) more restricted to MG1 grassland. The group C species are those which I normally associate with somewhat damper or more shaded conditions than those which prevail at the grazing trial, and may be found in the hedgebank flora or calcareous scrub for example. This group contains only two species and I therefore do not attempt to test my classification due to the tiny sample size. The species in group D are those for which I can offer no explanation other than dispersal limitation for their absence. This group contains only three species, two of which (*Leontodon hispidus* and *Trifolium dubium*) are examined experimentally in Chapters 4 and 5.

An examination of those species which have a low discriminant probability of occurrence (p<=0.64) but which are present in the grazing trial shows patterns suggestive of a link between phylogeny and community membership over and above the set of traits examined here, although the sample size is too small to draw firm conclusions. Of the 12 mispredictions in this category, all but three species (*Agrimonia eupatoria*: Rosaceae *Primula veris*: Primulaceae and *Cerastium glomeratum*: Caryophyllaceae) are either in the Asteraceae (*Crepis capillaris, C. vesicaria, Hypochaeris radicata, Leontodon*

autumnalis, *L. taraxacoides* and *Tragopogon pratensis*) or Ranunculaceae (*Ranunculus acris*, *R. bulbosus* and *R. ficaria*), despite the fact that the group of species as a whole is widely drawn from 28 different families.

Ecological Group	Species
Group A (ruderal herbs)	*Capsella bursa-pastoris* *Geranium molle* *Papaver rhoeas* *Plantago major* *Potentilla anserina* *Rumex obtusifolius* *Stellaria media*
Group B (tall herbs or sprawling species)	*Convolvulus arvensis* *Glechoma hederacea* *Heracleum sphondylium* *Hypericum perforatum* *Lamium album* *Leucanthemum vulgare* *Vicia sepium*
Group C (moist or shaded grassland herbs)	*Fragaria vesca* *Prunella vulgaris*
Group D (dispersal limited?)	*Lathyrus pratensis* *Leontodon hispidus* *Trifolium dubium*

Table 3.4. Species with a high discriminant probability (p>=0.65) of occurring in the grazing trial but which are absent. Group A species are those associated with disturbed or trampled ground, Group B with taller grassland, Group C more shaded or moist sites and Group D are those which may be dispersal limited. See text for more details.

3.5 Discussion

Trait magnitude

The flowering period variable TOTFLO showed a significant difference in magnitude, and a somewhat marginal result was recorded for FLO. The longer flowering period or greater period of flowering outside the summer grazing period was associated with presence within the grazing trial. This supports previous ideas about the management of the grazing trial, and suggests that a less intensive grazing regime would not only benefit the plants which are already there, but would lead to the establishment of a greater number of forb species. Abundance in the surrounding landscape yielded the most significant difference in trait value and is discussed below under the 'null model' heading. The other two significant trait

value differences (competitive ability COMP and nutrient tolerance/requirement NUTR) both yielded results in the expected direction. They suggest that the agricultural past of the site still leaves its mark on the vegetation today. With time, it seems possible that the dominance of the competitive species may decline, but there is little that can be done to hasten the process other than taking the drastic step of ploughing the sward, sowing (and removing) one or more crops under conditions of no fertiliser input and then reseeding the sward with a diverse seed mixture.

Non-significant results were obtained for both measures of plant height (MINHT and MAXHT), seed weight and seed bank (SDWT and SDBNK), ability to reproduce vegetatively (VEG) and both measures of longevity (ANN and LONGV). Possibly the lack of a significant relationship between plant height and presence in the grazing trial results from the fact that individual species can show a great deal of morphological plasticity under grazing (e.g. Diaz *et al.* 1992) which may be poorly reflected in the height data used here. Alternatively, the position of the growing shoots above ground or palatability of the species may be critical factors. Leishman and Westoby (1994b) note that a wide range of seed sizes may be found within a single plant community, a result which seems likely to account for the lack of a significant relationship in the case of SDWT. The absence of significant differences in longevity (LONGV and ANN) suggest that selection for longer-lived species in the grazing trial is at most rather weak. The other traits which showed non-significant differences are discussed below.

Under/overdispersion of traits

In the case of abundance (ABUND), strong trait underdispersion was detected. Marginal underdispersion was recorded for nutrient level (NUTR) and, very marginally, dispersal ability (DISP). Underdispersion is a by-product of the fact that trait *values* in one section of the scale (e.g. species with a high nutrient tolerance/requirement) are favoured. In these cases, the fact that no allowance was made for phylogeny appears unimportant, since the differences in magnitude of these variables was examined using phylogenetic methods.

With the exception (discussed below) of competitive ability (COMP), the other traits which showed significant differences in magnitude were also underdispersed although not significantly so. The overdispersion of traits, however, is not a by-product of selection for particular trait values but is *itself* the result of selection: the sifting and shuffling of species in such a way that the less similar are favoured. It is an important distinction which must be borne in mind if an attempt is being made to model community assembly in a comprehensive way. I return to this in Chapter 8. The only very marginally overdispersed trait found in this study was the ability to reproduce vegetatively, and the lack of a corresponding difference in value for this trait (Table 3.1) is perhaps important. In their study of the grassland plants of Miller's Dale, Derbyshire, Thompson *et al.* (1996) found that the species present in the community tended to be similar in terms of their traits as adult plants, but that there was greater separation between the species along a regeneration axis. The weak overdispersion reported here may be another manifestation of this principle, although a corresponding overdispersion was not recorded for seedweight (SDWT) or seedbank (SDBNK). A non-significant result, at least for SDBNK, may just reflect the relatively crude way in which this variable has been categorised. A detailed study by Olff *et al.* (1994), for example, showed a relationship between germination characteristics and species succession in grassland. For the other variables which showed neither differences in trait magnitude nor dispersion, it is hard to draw conclusions. The traits may play an important role in community assembly but were perhaps recorded in a way too crude or unsuitable to detect differences. Alternatively, the traits may be unimportant, at least for the site studied here.

It is worth considering these results in the light of the predictions offered by Weiher and Keddy (1995). The trait most obviously related to competition (COMP) was overdispersed as predicted, although not significantly so ($0.5<p<0.1$, 2-tailed test). Another trait, nutrient level (NUTR), which has been found to be positively related to absolute competitive intensity (Grace 1993) was underdispersed. The ability to reproduce vegetatively (VEG) was marginally overdispersed. This may be regarded as a trait closely linked with competition, since a highly competitive environment may yield few opportunities for

establishment by seed, but from the viewpoint of the establishing species, vegetative reproduction is a way of overcoming what (for it) amounts to environmental adversity. This highlights a practical difficulty in testing the hypotheses of Weiher and Keddy. Whilst the logic behind the hypotheses is clear, there can be great difficulty in deciding whether a trait is a 'competitive' or 'adversity' one.

The null model

All other things being equal, one would expect species which are more abundant in the wider landscape to be more likely to occur in the grazing trial. This expectation stems from the idea of random sampling, and it is useful to examine it in relation to the null model adopted here. Richardson *et al.* (1995) used a weighted (logarithmic) measure of species abundance in an attempt to allow for the unequal likelihood of species entering the community from the species pool, irrespective of other traits. In other words, they tried to take out the effects of abundance before examining the distribution of traits such as growth form. It would be possible (in theory) to adopt a similar approach here, but such an attempt founders on the difficulty of how to allow for abundance. In the case of the study by Richardson *et al.* (*op. cit.*), it is far from clear why a *logarithmic* weighting of the abundance (rather than a different weighting or, indeed, no weighting at all) removes the effect of unequal likelihood of species entering the community.

In addition to this difficulty, there is the further question of what one should give logical priority to in a null model of this kind. It might be argued that the effects of abundance should where possible be removed prior to examining trait differences because such correlations as may exist between abundance and the traits will simply confound matters. In the present case, however, the grassland community of the grazing trial is typical (in terms of species composition) of grasslands over much of lowland England, having been modified by modern agricultural practices (Chapter 2), and the question of why the abundant species are abundant both in the study site and the wider landscape has therefore to be considered. Presumably, they owe their abundance at least in part to the possession of certain traits, and the abundant species in the grazing trial are probably abundant for the same reasons that

they are abundant in many other grasslands. But if it is the case that certain traits are a cause of abundance, it makes at least as much sense to control for traits before examining abundance rather than the reverse. I have used a null model which rules out phylogenetic effects as much as possible, and then treats the other variables on an equal footing. I regard this as an appropriate one for the job, but it does serve to emphasise the point that null models have to be considered with care, and must be as relevant as possible to the question in hand (cf. Wilson 1995, see also Gotelli and Graves 1996).

Predicting presence and rank abundance

The discriminant function worked well in assigning species present in the grazing trial to their correct group, but it performed poorly in assigning the absent species to the right group. As discussed above (section 3.3.3), it is difficult to formulate a reliable rule for allocating species to two groups: present in a community or absent. But the direction of the imbalance in the allocation rule is of interest. Some of the species predicted to be present in the grazing trial although actually absent may just be errors resulting either from the use of an excessively simple model (linear discriminant function) or inadequate predictors. There is also the fact that the species pool was selected in such a way as to include some species which are probably unsuited to growth in the grazing trial under current management regimes (see below). The fact remains, however, that the grazing trial still appears to be slowly increasing in species diversity (Watt *et al.* 1996) following the cessation of fertiliser application in the early 1980's. It may be the case that some of the species erroneously predicted to be present would now be able to inhabit the site but have not yet colonised it due to dispersal limitation.

Some further light is shed on the assembly of this community by considering the correlation between the discriminant probabilities and species abundance. A highly significant positive relationship between the two was recorded. Figure 3.2 indicates that only species with a probability of about 0.65 or more of occurring in the grazing trial ever occur in any abundance. If this probability is taken as an empirically determined cut-off point, below which species are rare or absent but above which they may be present and perhaps

abundant, a study of the mispredictions is informative. The group A species are those typical of disturbed or trampled ground. Careful study of grazed grasslands in lowland England often reveals some of these species to be present (R. Tofts, pers. obs.), although their occurrence is often patchy. There appear to be suitable microsites for the species in the grazing trial, although such microsites are scarce. They occur in areas scuffed or trampled by sheep (e.g. around water butts), old molehills and other small areas of disturbance. Some species of disturbed ground such as *Rumex crispus* and *Veronica arvensis* are indeed present (but rare) in the grazing experiment. For these reasons I regard the group A species as being potential community members which are probably absent simply because suitable micro-sites are limited, and seed dispersal of these species into the site is probably insufficient for them to establish and maintain themselves in the community. These mispredictions are, perhaps, best regarded as reasonable mistakes: species which may well be able to sustain themselves in the community, at least for a limited time, but can not (under present management regimes) be expected to occur in any abundance. The group B species appear unsuited to conditions at the grazing trial, and I therefore regard their predicted presence as an error. They are normally associated with rank vegetation. These erroneous predictions are likely to have arisen partly because of the way the species pool was drawn up, making no assumptions about management other than it should be such as to retain the grassland character of the site. This was a necessary step in order to examine the effects of the current management regime on community composition. If, however, the primary aim were to predict the abundance of species in the community as it is managed now, a more narrowly defined species pool is likely to lead to better predictions. The group C species are those I associate with damper or more shaded conditions, but because there are only two species in this group, it is difficult to draw any conclusions from their predicted presence. The group D species are those for which I would regard the conditions in the grazing trial as being suitable, and the only explanation for their absence I can offer is that of dispersal limitation. This explanation is therefore similar to that offered for the group A species, although it differs in one important respect. For the group D species, the greater part of the sward appears to offer a suitable environment and once initially established, the plants may be expected to maintain themselves without further seed

input from outside. In contrast, suitable sites for the group A species are probably scarce and several of the species are short-lived. For these species to maintain themselves, a regular seed rain from outside the site is likely to be required to balance extinction in some microsites with establishment in others.

Of the species group with a lower (p<=0.64) discriminant probability but present in the grazing trial, those in the Asteraceae are species with wind dispersed seeds. This might hold the explanation for their presence. It is harder to speculate about the reasons for the presence of the other species in the grazing trial, although fruits of *Agrimonia eupatoria* are animal dispersed. Dispersal mechanism was insignificant as a predictor of species occurrence (Table 3.1) when an overall assessment was made, but this may have been due to its effects being masked by other more important traits, or the fact that a coarse classification of dispersal modes had to be used. Species with awned propagules may be very much poorer dispersers than those with a pappus for example, but this distinction was not made in the trait matrix. Alternatively, given the occurrence of most of these species in just two families, their presence may be a result of other phylogenetically linked traits which were not examined.

The model used here to predict species presence or abundance in the community gave results which were significantly better than random allocation, but which were far from perfect. As mentioned above, a more tightly circumscribed species pool may lead to better predictions. Apart from this possibility, how might predictions be improved?

First, the traits used to make the predictions need to be considered. The ones used here were taken from published sources and were categorised in a rather crude way. Both the acquisition of information on more traits and less crudely categorised data might be expected to improve predictive power. In Chapter 7, for example, I examine experimentally the performance of two species in relation to different levels of defoliation and nutrients. This work suggests that subtle differences in plant characteristics (a difference in young leaf attitude in this case) may lead to significant differences in plant performance and, as a

consequence, affect community assembly. But if the finding that subtle differences can cause important effects is of general applicability, adequately categorising a large set of species on the basis of their traits will be an immense task.

Second, there is the matter of the model. The linear discriminant function used here is one of the simplest methods to implement, and is therefore a good starting point. It also fulfils the criteria suggested by Keddy (1992) for a method of predicting species presence in a habitat. The extent to which the performance of a simple linear model like this can be improved by the addition of further traits or more sensitively quantified ones remains to be seen. But a model with fewer constraints may offer better predictive power. If communities are assembled in a complicated fashion as has been argued elsewhere (see e.g. Diamond 1975, Haefner 1978, 1981) it will be impossible for a simple linear function to model this complexity. In order to develop a comprehensive model of plant community assembly, the structure and logical relationships between the various processes which affect community assembly must be recognised. I have suggested (section 3.2.1) that the assembly of forbs and graminoids into communities may follow different rules and therefore may best be described or predicted by different models. It is, however, equally possible that the diverse array of forbs examined here is organised into various groups, the assembly of which may best be modelled differently (see Chapter 8).

Beyond matters of models and data, however, lies the messy inscrutability of nature. How predictable is the assembly of communities even given the perfect model and unlimited data (Fowler 1990)? The way environmental variability causes biological invasions of fresh water systems to proceed in idiosyncratic ways has been discussed by Moyle and Light (1996), and similar effects are to be expected in the case of terrestrial plant community assembly. I return to matters of models, data and unpredictability in Chapter 8.

Chapter 4. Barriers to colonisation from the species pool: dispersal, germination and establishment

4.1 Introduction

In the previous chapter I examined the relationship between traits and the presence or abundance of plant species in the grazing trial. A significant relationship between the two was detected for at least some traits, but some species were predicted to be present in the study community whilst observation shows them to be absent (or, in one case, predicted to be absent but in fact present). This leads on to the question 'how predictable is community assembly?' In this and the following chapter, I investigate experimentally some of the ideas suggested by the work in Chapter 3. I compare the performance of five pairs of congeners, one member of each pair being already present in the grazing trial and the other absent. In the absence of dispersal limitation, if there is strong post-dispersal selection for species which are adapted to conditions in the grazing trial, one would expect those congeners which are already present to outperform those which are absent. If dispersal limitation plays an important role, then the relationship between plant performance and 'natural' presence or absence is likely to be less clear cut. There are two main questions which I wish to investigate here: *i)* do the species naturally present in the grazing trial outperform those which are not? *ii)* what effects do the different combinations of management have on plant performance, and are the different species affected in the same way?

A plant species may fail to occur in a community for many reasons which can operate at any stage in the life-cycle from seed dispersal through establishment to reproduction. Two potentially important stages at which species may be filtered out are propagule dispersal

into the community (i.e. dispersal limitation, see e.g. Tilman 1997, Primack and Miao 1992, Ackerman *et al.* 1996, Herrera 1991) and the early stages of growth after germination (e.g. Fenner 1987, Oliveira Silva 1992, Herrera 1991, Hanley *et al.* 1995). The creation of gaps in the sward may be important in allowing new species to gain a foothold in a grassland community during the early stages of colonisation (e.g. Bullock *et al.* 1994 and 1995). In this chapter I restrict myself to comparing plant performance from the stage of germination to the development of two true-leaves (or whorls of leaves), and I investigate performance over the later stages of growth in Chapter 5. The field experiment described below (section 4.2.3) allows an assessment to be made about the effects of dispersal limitation, mortality in the early stages of growth, grazing regime and gaps on the establishment of a selected group of species in the Little Wittenham grazing trial. In making an assessment of barriers to species establishment at the germination stage, it is helpful to have information about seed viability as determined in the laboratory. For this reason, a growth cabinet study on seed viability was undertaken as described in section 4.2.2.

4.2 Methods

4.2.1 Selecting the study species

One obvious way of investigating the role of dispersal limitation is to introduce new species to the grazing trial and to monitor what happens. A complication with such an approach, however, is that negative results can be uninformative. If several new species are introduced to a site and they fail to establish, this may be because they are in some way not suited to conditions there, or it may be because the methods used to establish them were unsuitable (e.g. poor planting technique). There is also the difficulty in a short-term study such as this of interpreting what the results mean for plants in nature. If 100 seeds are planted, 10 germinate and five reach the stage of showing two true leaves, is this a good result in terms of plant establishment? What is it likely to mean for the composition of the community? To circumvent these difficulties, the approach taken here was to identify congeneric pairs from the local species pool, one of which already grows in the grazing trial

and one of which does not. The choice of congenerics means that phylogenetic effects on the likelihood of establishment can be ruled out. The pair-wise selection of species means that the species naturally present in the grazing trial acts as a 'yardstick' against which the success of establishment of its congener can be measured.

Five suitable pairs of congeners (listed in Table 4.1) were selected from the species pool.

Present within grazing trial	**Not present within grazing trial**
Leontodon autumnalis	*Leontodon hispidus*
Rumex crispus	*Rumex obtusifolius*
Cirsium vulgare	*Cirsium eriophorum*
Trifolium pratense	*Trifolium dubium*
Galium aparine	*Galium verum*

Table 4.1. Congeneric pairs used in the studies described in this and the following chapter. The left hand column lists those species already present in the grazing trial, whilst the right hand column lists species present in the species pool but absent from the grazing trial.

The amount of work involved in the experimental studies made it impossible to study more than five species pairs. The congeners listed in Table 4.1 were selected because they both represent species for which seed could either be bought or harvested by hand, and they belong to several different families. The latter consideration is important if one wishes to discover whether general rules about species establishment apply, since this can only be properly tested if the study species represent a broad range of plant types. These 10 species were used in the studies described in both this and the following chapter.

4.2.2 Laboratory experiments

Germination of the five species pairs was investigated in a growth cabinet at a steady temperature of 20°C, in order to assess the viability of the seeds used in the field experiment. Due to limitations of space, the species were assessed in a pair-wise manner. For each species pair, two experimental conditions were imposed: *i)* dark (blackened petri dish) and *ii)* light (100 microeinsteins m^{-2} s^{-1}). The germination of seeds may be affected by various types of treatment (Hendry and Grime 1993), but a fuller investigation than that undertaken here would have been too labour intensive. The choice of light and dark

treatments is therefore a compromise between a single estimate of viability and the more complete information yielded by projects such as the integrated screening programme (Hendry and Grime *op cit.*). Two replicates of each condition were used for each species, with 50 seeds being placed on filter paper in each 90 mm diameter petri dish. Thus 200 seeds of each species were required, 100 (50 x 2) for the light treatment and 100 for the dark treatment. For each species pair, the petri dishes were randomly positioned in the growth cabinet, and the filter paper was kept moist with distilled water. Seeds of the two *Trifolium* species were lightly scarified before being placed in the petri dishes. The pappus was removed from the *Cirsium* and *Leontodon* fruits, and the perianth segments were removed from the *Rumex* nuts before being placed in petri dishes. The source of seed for the five pairs of species is shown at Table 4.2.

Preliminary analysis of the data from the germination experiment indicated that the standard ANOVA assumptions were met, and the data were analysed as a completely randomised 2 x 2 factorial design.

Species	Seed source
Galium aparine	Walton Hall, Milton Keynes. SP 884370
G. verum	Emorsgate seeds. Norfolk
Trifolium pratense	Emorsgate seeds. Wiltshire
T. dubium	Emorsgate seeds. Norfolk
Rumex crispus	Walton Hall, Milton Keynes. SP 884370
R. obtusifolius	Walton Hall, Milton Keynes. SP 884370
Cirsium vulgare	Roadside verge, nr. Buckingham. SP 780323
C. eriophorum	Hill End Farm, Oxford. SP465073
Leontodon autumnalis	John Chambers seeds. Somerset
L. hispidus	Emorsgate seeds. Somerset

Table 4.2. Seed sources for the 10 study species. For the seeds collected by hand, the 6-figure grid reference is given. For purchased seeds, the provenance of the material is given.

4.2.3 Field experiments

In order to keep the experiments to a manageable size, only the spring-grazed paddocks were used, and the grazing trial was thus reduced to a 2 x 2 factorial design in two blocks (i.e. eight paddocks in total). The spring grazed paddocks were selected because those

which are ungrazed in the spring tend to be species-poor, and the likelihood of at least some of the planted species germinating and growing successfully is probably greatest in those which receive spring grazing. In each of the eight paddocks, two sub-blocks were located at random subject to the constraint that they avoided a 10 metre boundary and the central

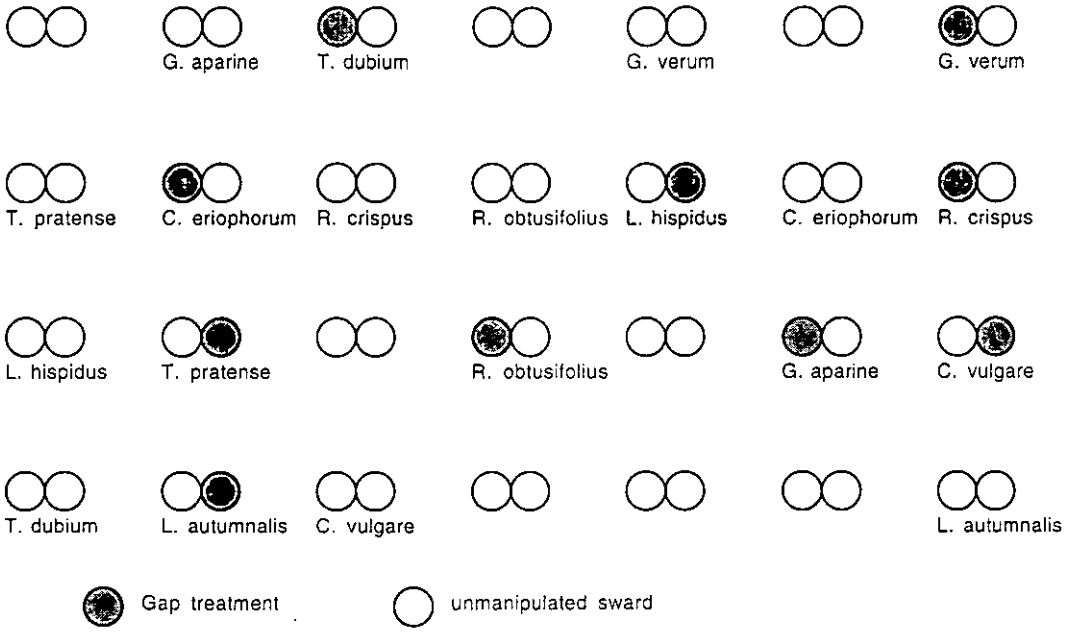


Figure 4.1. Example of experimental layout. Shaded circles indicate sown plots, unshaded circles represent control plots. Unlabelled circles represent extra plots. See text for further details.

part of the paddock in which two permanent quadrats were located. Each of the two sub-blocks comprised 28 paired plots (one planted and one control, the arrangement being randomised) spaced at 1 metre intervals on a 7 x 4 grid. The control plots were used to estimate the amount of germination occurring naturally. The positions of the plots were permanently marked using two 22 mm (internal diameter) plastic pipes hammered into the ground at a distance of 28 cm apart. Two metal legs of a planting frame (Treweek 1990) were fitted into the pipes to locate the plot whenever monitoring was undertaken. An example of the experimental layout in one sub-block is shown at Figure 4.1. The locations of species and treatments were randomised in all cases. Two blocks were set up in each paddock to provide a degree of insurance against destruction of sites (e.g. by molehills) rather than to provide an estimate of the variability within each paddock. This precaution proved unnecessary, and the analyses reported here are based upon the average result for the two sub-plots in each paddock. Similarly, 28 sites per plot were created although there was only an obvious need for 20 (10 species x 2 treatments - see below) to allow extra sites if any parts of the experiment had to be repeated. In the event, some extra sites were required. Within this framework, the following study was undertaken.

The sowing experiments were undertaken in autumn 1996 (17 October to 14 November). Two plot treatments were used: *i)* native sward, and *ii)* bare ground (gap). The bare ground was created by spraying out 33 cm diameter circular patches in the sward with glyphosate on 31 August 1996, using a plant pot of the required diameter with the bottom removed to shield the surrounding vegetation from spray drift. The herbicide was seen to take effect within about two weeks, and after 6 weeks the dead vegetation was cut back to ground level using scissors and removed, taking care to disturb the soil as little as possible. This treatment produced a similar area of bare ground to that which occurs naturally at the site as a result of molehills which subsequently become flattened by a combination of rain and sheep trampling. Each species pair was sown together over one or two (consecutive) days. Prior to sowing, the seeds were treated (pappus removal etc.) as described above. Initially, for each species 100 (150 in the case of *Leontodon*) seeds per plot were mixed

with 5 cm^3 of fine sand, and sprinkled as evenly as possible using a shaker like a large pepper pot within a circular plot of 22 cm diameter (centred on the larger 33 cm diameter gap in the case of the bare ground treatment). Again, a plant pot with the bottom removed was used to confine the seed within the required radius. Each control plot was 'sown' with the 5 cm^3 of sand alone. After sowing, the plots were lightly watered to help the seed make contact with the ground. In the case of the *Cirsium* species, however, this method of sowing was found to result in very heavy seed predation by small mammals. This part of the experiment was therefore repeated with 81 seeds of these two species being planted into the soil in each sown plot with tweezers on a 9 x 9 grid at 2 cm spacing, using four of the extra pairs of plots in each block selected at random.

The seed plots were monitored on approximately every 7-14 days throughout the winter and until mid-May 1997 (after which no further emergence was noted), except in periods of particularly harsh weather when casual observation revealed little or no evidence of new germination. Due to the amount of work involved, however, not all species could be monitored on each visit. The procedure adopted was to randomly check selected plots of each species, determine which species pairs had shown the greatest change in numbers since the previous visit, and monitor those species fully. Congeners were, however, always recorded on the same visit. On germination, every seedling was marked with a small dot of acrylic paint. This method was found to mark the seedlings in a permanent way without damaging them. The seedlings were allowed to grow until they reached the two true-leaf stage (or, in the case of *Galium*, two whorls of leaves) at which time they were removed from the plot to avoid excessive interference with the other seedlings. Two variables were therefore recorded for each sown plot: *i)* the number of seeds germinating, and *ii)* the number reaching the two true-leaf (or two leaf whorl) stage. The corresponding numbers obtained from the adjacent control plot were deducted to allow for natural germination, and the analysis was performed on these corrected totals. Only in the case of *Cirsium vulgare* did the control plots show any natural germination, and even in this case it was very patchy.

An initial analysis of the data indicated that the standard ANOVA assumptions were met, although the analysis is still relatively complex due to the experimental design adopted. Having omitted those paddocks which are ungrazed in spring, the main grazing experiment is a 2 x 2 factorial design in two blocks. Within each paddock, however, there are two further treatments: *i)* species and *ii)* gap/native sward, creating a split-plot design (see e.g. Mead and Curnow 1983). The fact that one would expect a positive correlation between the two variables recorded (number of seeds germinating and number reaching the two true-leaf stage) introduces a further complication. For each species pair, a split-plot multivariate analysis of variance (MANOVA - see e.g. Krzanowski 1988) was therefore undertaken to determine the nature of the experimental effects and their significance.

In the results section, mean values are reported. These have been obtained in the standard way by averaging them over all the other treatments for which no significant effects were detected. The only exceptions to this are the results for *Leontodon* which are explained separately below.

4.3 Results

4.3.1 Laboratory germination

The percentage germination under light and dark conditions for the five pairs of congeners is given at Table 4.3. Statistically significant ($p<0.05$) differences between species were recorded for *Trifolium*, *Rumex* and *Leontodon*, although only in the latter case was the difference very marked, with *L. autumnalis* showing 1-2% germination and *L. hispidus* showing 80-83%. *Rumex crispus* showed slightly better germination than *R. obtusifolius* (a mean germination of 96% *vs.* 89% in the light treatment and 94% *vs.* 76% in the dark treatment). *Trifolium dubium* showed somewhat better germination than *T. pratense* (95.5% *vs.* 81.5%). The two pairs of *Galium* and *Cirsium* congeners showed no differences in germination between species or light treatment.

Only for *Rumex obtusifolius* was the difference between light and dark treatments statistically significant, with 76% germination in the dark and 89% in the light.

Species	Dark germination (%)	Light germination (%)
Galium aparine	56^{a}	72^{a}
Galium verum	77^{a}	84^{a}
Trifolium pratense	78^{a}	85^{a}
Trifolium dubium	95^{b}	96^{b}
Rumex crispus	94^{a}	96^{a}
Rumex obtusifolius	76^{c}	89^{d}
Cirsium vulgare	93^{a}	85^{a}
Cirsium eriophorum	93^{a}	85^{a}
Leontodon autumnalis	1^{a}	2^{a}
Leontodon hispidus	80^{b}	83^{b}

Table 4.3. Percentage germination for the five pairs of congeners in growth cabinet tests. Figures with the same superscript *within each congeneric group* do not differ significantly ($p>0.05$) from one another. The central column gives the percentage germination in darkness, the right hand column gives percentage germination in the light.

4.3.2 Field experiments

The results of the split plot MANOVAs for the five pairs of congeners are shown at Tables 4.4 to 4.8. To save space, the sums of squares and products matrices for the various treatments (the multivariate equivalent of the treatment sums of squares found in a univariate ANOVA) are not shown here. The tables distinguish main plot and subplot treatments, and give values of the test statistic Wilk's lambda (λ) together with the appropriate *p*-value. For simplicity, main effects and interactions found to be significant in the multivariate case are shown graphically in terms of their univariate effects on the number of seeds germinating and number of plants reaching the two true-leaf stage separately at Figures 4.2 - 4.6.

	Treatment	df	Wilk's λ	Significance
Main Plot	Block	1	0.4901	p=0.4901
	Summer (S)	1	0.7584	p=0.7584
	Winter (W)	1	0.5177	p=0.5177
	S x W	1	0.5379	p=0.5379
Subplot	Gap (G)	1	0.9215	p=0.6379
	Species (Sp)	1	0.7668	p=0.2321
	G x Sp	1	0.5335	***p=0.0316***
	S x G	1	0.6304	p=0.0790
	S x Sp	1	0.7300	p=0.1771
	W x G	1	0.6540	p=0.0968
	W x Sp	1	0.4189	***p=0.0083***
	W x S x G	1	0.8548	p=0.4219
	W x S x Sp	1	0.5806	p=0.0503
	W x G x Sp	1	0.9666	p=0.8296
	S x G x Sp	1	0.6731	p=0.1134
	W x S x Sp x G	1	0.6580	p=0.1000

Table 4.4. MANOVA for *Galium* experiment. Main effects and interactions are shown in the second column, degrees of freedom in the third and values of the test statistic Wilk's λ in the fourth. The significance of the treatment effects is shown in the last column (values with p<0.05 shown in bold). Bonferroni corrected 5% cut-off point at p=0.0051.

	Treatment	df	Wilk's λ	Significance
Main Plot	Block	1	0.8114	p=0.8114
	Summer (S)	1	0.4805	p=0.4805
	Winter (W)	1	0.8901	p=0.8901
	S x W	1	0.6577	p=0.6577
Subplot	Gap (G)	1	0.6672	p=0.1080
	Species (Sp)	1	0.2331	**p=0.0003**
	G x Sp	1	0.6998	p=0.1404
	S x G	1	0.7507	p=0.2066
	S x Sp	1	0.8116	p=0.3172
	W x G	1	0.9850	p=0.9202
	W x Sp	1	0.8806	p=0.4969
	W x S x G	1	0.8748	p=0.4792
	W x S x Sp	1	0.8941	p=0.5403
	W x G x Sp	1	0.8689	p=0.4617
	S x G x Sp	1	0.7784	p=0.2521
	W x S x Sp x G	1	0.9546	p=0.7745

Table 4.5. MANOVA for *Trifolium* experiment. Main effects and interactions are shown in the second column, degrees of freedom in the third and values of the test statistic Wilk's λ in the fourth. The significance of the treatment effects is shown in the last column (values with p<0.05 shown in bold). Bonferroni corrected 5% cut-off point at p=0.0051.

	Treatment	df	Wilk's λ	Significance
Main Plot	Block	1	0.6055	p=0.6055
	Summer (S)	1	0.6126	p=0.6126
	Winter (W)	1	0.5971	p=0.5971
	S x W	1	0.4909	p=0.4909
Subplot	Gap (G)	1	0.3765	***p=0.0046***
	Species (Sp)	1	0.5135	***p=0.0256***
	G x Sp	1	0.6803	p=0.1202
	S x G	1	0.9116	p=0.6011
	S x Sp	1	0.8255	p=0.3483
	W x G	1	0.7739	p=0.2442
	W x Sp	1	0.9999	p=0.9995
	W x S x G	1	0.9841	p=0.9156
	W x S x Sp	1	0.9835	p=0.9126
	W x G x Sp	1	0.9589	p=0.7939
	S x G x Sp	1	0.8907	p=0.5291
	W x S x Sp x G	1	0.9735	p=0.8627

Table 4.6. MANOVA for *Rumex* experiment. Main effects and interactions are shown in the second column, degrees of freedom in the third and values of the test statistic Wilk's λ in the fourth. The significance of the treatment effects is shown in the last column (values with $p<0.05$ shown in bold). Bonferroni corrected 5% cut-off point at p=0.0051.

	Treatment	df	Wilk's λ	Significance
Main Plot	Block	1	0.5354	p=0.5354
	Summer (S)	1	0.4960	p=0.4960
	Winter (W)	1	0.7751	p=0.7751
	S x W	1	0.5399	p=0.5399
Subplot	Gap (G)	1	0.0832	**p=0.0000**
	Species (Sp)	1	0.0639	**p=0.0000**
	G x Sp	1	0.1062	**p=0.0000**
	S x G	1	0.4929	***p=0.0204***
	S x Sp	1	0.5749	***p=0.0476***
	W x G	1	0.9954	p=0.9750
	W x Sp	1	0.7059	p=0.1473
	W x S x G	1	0.6730	p=0.1133
	W x S x Sp	1	0.6234	p=0.0743
	W x G x Sp	1	0.8234	p=0.3434
	S x G x Sp	1	0.5418	***p=0.0344***
	W x S x Sp x G	1	0.7500	p=0.2055

Table 4.7. MANOVA for *Cirsium* experiment. Main effects and interactions are shown in the second column, degrees of freedom in the third and values of the test statistic Wilk's λ in the fourth. The significance of the treatment effects is shown in the last column (values with $p<0.05$ shown in bold). Bonferroni corrected 5% cut-off point at p=0.0051.

	Treatment	df	Wilk's λ	Significance
Main Plot	Block	1	0.2815	p=0.2815
	Summer (S)	1	0.0278	***p=0.0278***
	Winter (W)	1	0.1047	p=0.1047
	S x W	1	0.0407	***p=0.0407***
Subplot	Gap (G)	1	0.0204	**p=0.0000**
	Species (Sp)	1	0.0637	**p=0.0000**
	G x Sp	1	0.0204	**p=0.0000**
	S x G	1	0.9074	p=0.5860
	S x Sp	1	0.5627	***p=0.0423***
	W x G	1	0.7831	p=0.2606
	W x Sp	1	0.7511	p=0.2072
	W x S x G	1	0.6495	p=0.0932
	W x S x Sp	1	0.6496	p=0.0932
	W x G x Sp	1	0.7831	p=0.2606
	S x G x Sp	1	0.9074	p=0.5860
	W x S x Sp x G	1	0.6495	p=0.0932

Table 4.8. MANOVA for *Leontodon* experiment. Main effects and interactions are shown in the second column, degrees of freedom in the third and values of the test statistic Wilk's λ in the fourth. The significance of the treatment effects is shown in the last column (values with $p<0.05$ shown in bold). Bonferroni corrected 5% cut-off point at p=0.0051.

4.3.2.1 *Galium*

The *Galium* MANOVA is shown at Table 4.4. The effects of gap, species and winter grazing regime were found to be marginally significant in the form of the two interactions shown at Figure 4.2. In the absence of winter grazing, *Galium verum* outperforms *G. aparine* (mean number germinating = 48.8 per plot, mean number reaching two true leaves = 27.8 per plot *vs.* 24.6 and 14.4 respectively), but the reverse is the case in paddocks which are winter grazed (mean number germinating = 33.1 per plot, mean number reaching two true leaves = 13.9 per plot *vs.* 38.1 and 22.5 respectively). In the native sward, *G. verum* outperforms *G. aparine* (mean number germinating = 44.4 per plot, mean number reaching two true leaves = 22.3 *vs.* 25.0 and 14.4 respectively) but the situation is reversed in gaps (mean number germinating = 37.5 per plot, mean number reaching two true leaves = 16.4 *vs.* 37.8 and 22.5 respectively).

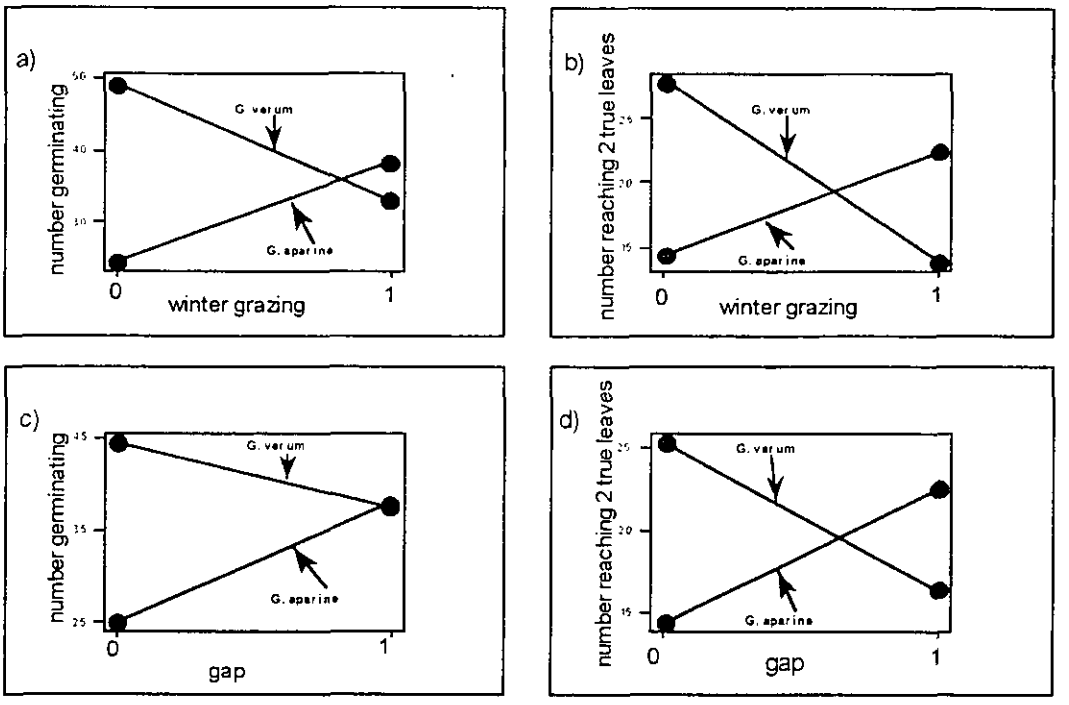


Figure 4.2. Interaction plots for *Galium* experiment. a) and b) interaction between winter grazing and species on number germinating and reaching the 2 true-leaf stage. c) and d) interaction between species and gap on number germinating and reaching the 2 true-leaf stage.

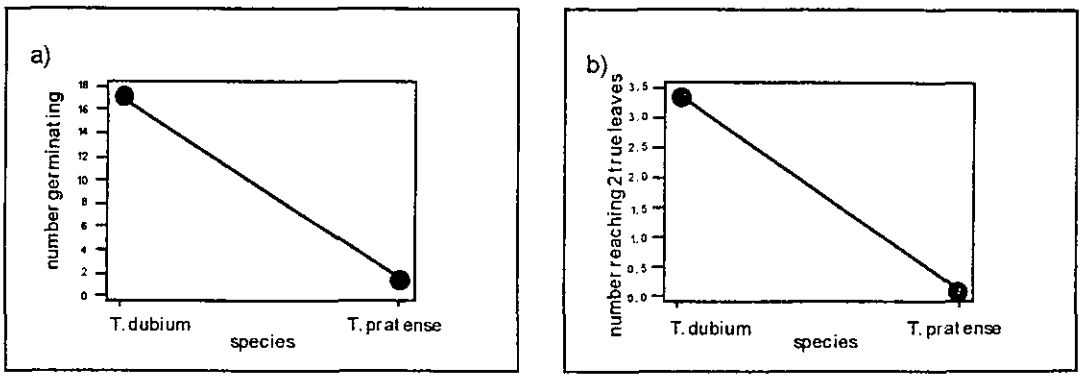


Figure 4.3. Main effects plots for *Trifolium* experiment. a) and b) species effect on number germinating and reaching the 2 true-leaf stage.

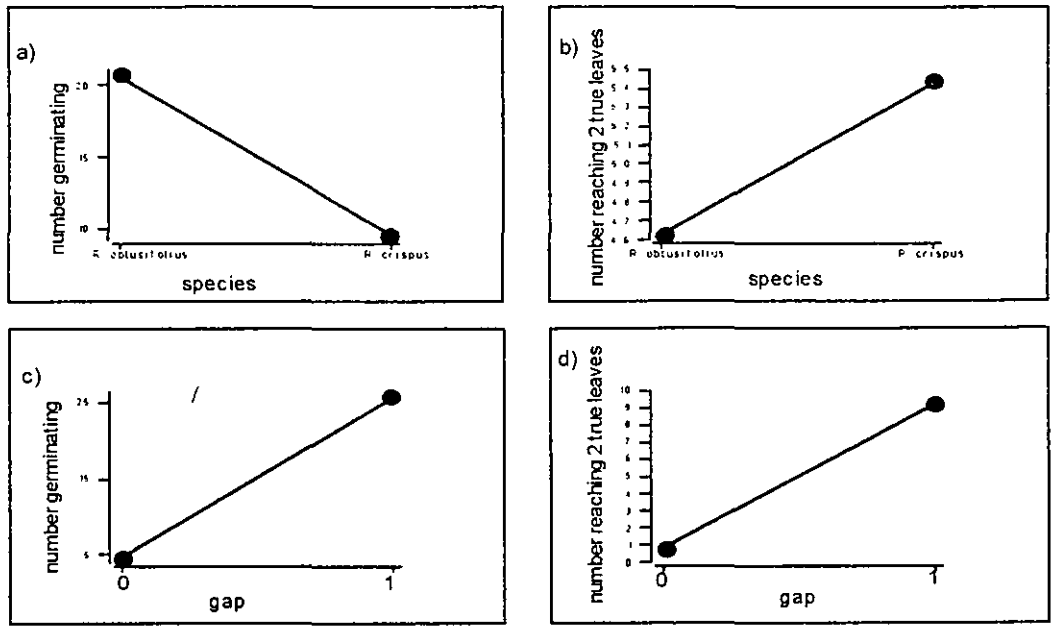


Figure 4.4. Main effects plots for *Rumex* experiment. a) and b) species effect on number germinating and reaching the 2 true-leaf stage. c) and d) gap effect on number germinating and reaching the 2 true-leaf stage.

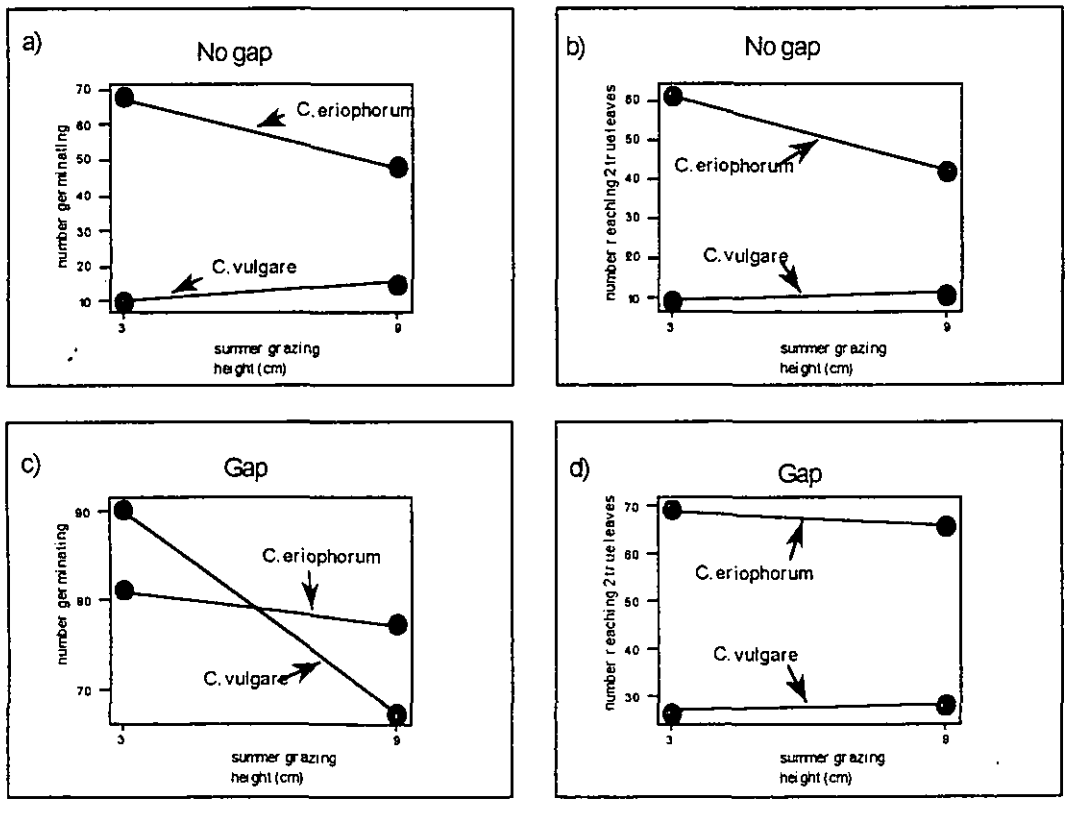


Figure 4. 5. Interaction plot for *Cirsium* experiment. a) and b) interaction between species and summer grazing intensity for germination and number reaching 2 true-leaves in the native sward. c) and d) interaction between species and summer grazing intensity for germination and number reaching 2 true-leaves in gaps. Patterns differ at $p < 0.05$.

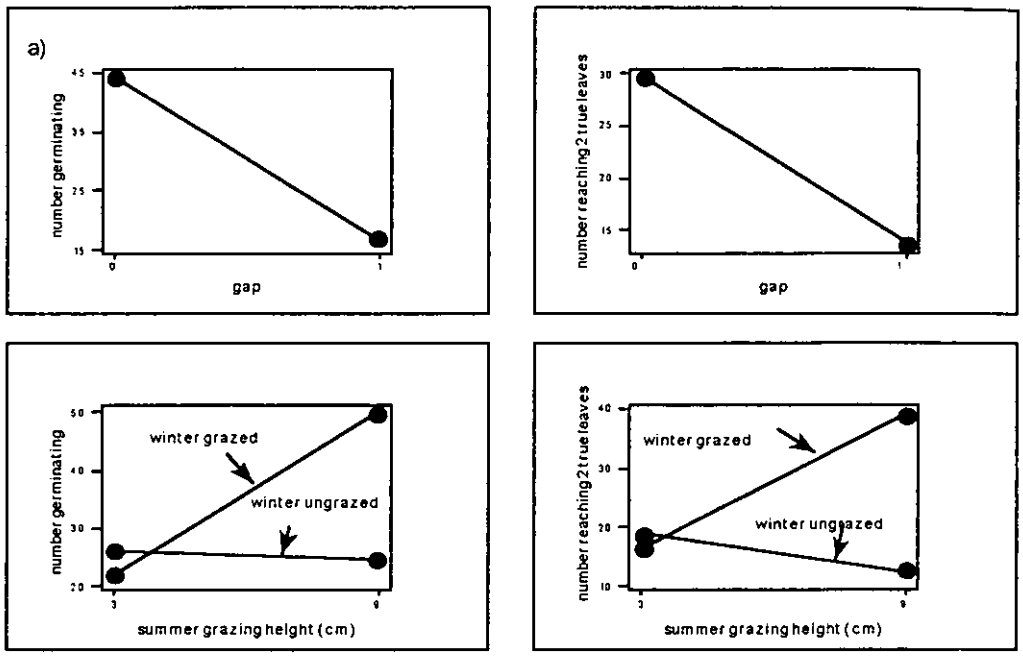


Figure 4.6. Main effects and interaction plots for *Leontodon hispidus*. a) and b) main effect of gap treatment on number germinating and number reaching 2 true-leaves. c) and d) interaction between summer and winter grazing on number germinating and number reaching 2 true-leaves.

4.3.2.2 *Trifolium*

The *Trifolium* MANOVA is shown at Table 4.5. The only significant difference detected was that between species, with *Trifolium dubium* performing substantially better than *T. pratense* (mean number germinating = 17.4 per plot, mean number reaching two true leaves = 3.4 per plot *vs.* 1.5 and 0.1 respectively). This is shown at Figure 4.3.

4.3.2.3 *Rumex*

The *Rumex* MANOVA is shown at Table 4.6. Marginally significant results were recorded for gap and species, and are shown graphically at Figure 4.4. Both species showed a substantially better performance in gaps compared with the native sward (mean germination = 25.8 *vs.* 4.5 per plot, mean number reaching two true leaves = 9.3 *vs.* 0.8 per plot). More

individuals of *R. obtusifolius* were found to germinate compared with *R. crispus* (20.8 *vs.* 9.5), although this difference disappeared at the two true-leaf stage when no significant differences between the two species remained (univariate ANOVA not presented here).

4.3.2.4 *Cirsium*

The *Cirsium* MANOVA is shown at Table 4.7. Terms involved in the significant or marginal effects are gap, species and summer grazing. They all feature in a three-way interaction. This interaction is best understood graphically, and is shown at Figure 4.5. *Cirsium eriophorum* generally outperforms *C. vulgare* both in terms of number germinating and number reaching two true leaves. The situation is reversed, however, in gaps subject to 3 cm summer grazing. Performance in gaps for both species always exceeded that in the native sward, although the precise extent to which gaps were beneficial depended upon the levels of other experimental treatments.

4.3.2.5 *Leontodon*

The *Leontodon* MANOVA is shown at Table 4.8. A highly significant species effect was recorded, simply reflecting the fact that no individuals of *L. autumnalis* were recorded from the field experiment. Laboratory germination of this species was very poor, and the poor field performance doubtless reflects the low viability of the seed. Two significant or marginal species interactions (species x gap and species x summer grazing) were detected, but these simply reflect the fact that numbers of *L. hispidus* varied under different gap and summer grazing regimes whilst numbers of *L. autumnalis* remained constant at zero. These results are therefore not discussed further. The mean results for *Leontodon* reported below are given as means averaged over non-significant treatments for *L. hispidus* alone. Marginally significant summer and winter grazing effects were observed in the form of an interaction and a significant gap main effect was recorded, as shown at Figure 4.6. Numbers of *L. hispidus* plants germinating and surviving to two true leaves were greater in the native sward compared to gap treatments (mean number of seeds germinating = 44.2

per plot, mean number reaching two true leaves = 29.6 per plot, *vs.* 17.2 and 13.6 respectively). In the absence of winter grazing, the performance of *L. hispidus* is broadly similar under both summer grazing regimes (mean number germinating = 26.2 per plot, mean number reaching two true leaves = 18.6 per plot for 3 cm summer grazing *vs.* 24.6 and 12.6 respectively for 9 cm summer grazing). In the presence of winter grazing, the effects of summer grazing are markedly different (mean number germinating = 22.2 per plot, mean number reaching two true leaves = 16.6 per plot for 3 cm summer grazing *vs.* 49.8 and 38.8 respectively for 9 cm summer grazing).

4.4 Discussion

The purposes of this experiment were twofold. The first question I posed (do the species which already occur in the grazing trial perform better than those which are absent?) requires a comparison between the performance of the congeneric pairs. The second question (what effects do the different combinations of management have on plant performance, and are the different species affected in the same way?) requires a comparison of the main effects of, and interactions between, the different experimental treatments for the different species pairs.

Congeneric comparisons

It is noteworthy that all five species which do not occur as part of the native vegetation of the experiment equalled or outperformed their congeners under at least one combination of experimental conditions. This fact begs the question of why the (actually or apparently) inferior performer is sometimes the one present in the grazing trial. This question can best be answered when information is also available about performance in the later stages of the life-cycle, and I leave discussion about this until the following chapter. All mention of species performance below is therefore restricted to the early stages of growth investigated here.

Leontodon hispidus and *Trifolium dubium* both outperformed their congeners under all circumstances. In the case of *Leontodon*, the difference in performance was predictable on the basis of the laboratory germination experiments in which *L. autumnalis* showed very poor viability. It seems most likely that this low viability is a result of poor seed stock rather than an intrinsic property of the species, but this part of the experiment does at least show that *L. hispidus* is capable of germinating and reaching the two true leaf stage in the grazing trial. Numbers of *L. hispidus* individuals germinating and reaching two true leaves were greater under certain treatments than those for some other species including ones which are naturally present in the grazing trial (e.g. *Trifolium pratense* and *Rumex crispus*).

Trifolium dubium was found very markedly to outperform *T. pratense* under all experimental conditions. *T. dubium* showed slightly (17%) better germination in the laboratory than *T. pratense*, but the vast difference in performance between the two species (over a 10-fold increase in numbers germinating and 30-fold increase in numbers reaching the two true leaf stage) suggests that seed viability is not the primary cause. Observations made during the course of the fieldwork suggest a partial explanation for this result. Seeds of *T. pratense* are conspicuously larger than those of *T. dubium* and perhaps more visible to, or sought after by, seed predators. Whilst monitoring the experiment, many seeds of *T. pratense* were seen to have been cracked open, apparently by small mammals, whilst none of the *T. dubium* seeds was seen to have suffered in this way. It therefore seems likely that differential seed predation is an important cause of the difference in species performance. This has been shown to vary greatly between species and can be considerable (Hulme 1994).

Significantly more individuals of *Rumex obtusifolius* germinated than did those of *R. crispus*, despite the latter species being the one already present in the grazing trial and also showing slightly better laboratory germination. This difference, however, had disappeared by the two true leaf stage. Some slug damage to *Rumex* seedlings was noted, and *R. obtusifolius* was found to germinate more quickly in the field than *R. crispus*. Observations in the field suggest that the germination of *R. obtusifolius* coincided with a period of greater

slug activity than did that of *R. crispus*, and this may account for the similarity in performance of the species by the two true leaf stage.

Cirsium eriophorum outperformed its congener *C. vulgare* under all circumstances except in gaps subject to 3 cm summer grazing, an interesting result given that *C. vulgare* occurs naturally in considerable abundance in many of the paddocks. *C. eriophorum* has substantially bigger seeds than *C. vulgare*, and this fact may account for its generally superior performance, especially in the non-gap treatments (cf. Westoby *et al.* 1996, Armstrong and Westoby 1993). This contrasts with the finding for the *Trifolium* congeners, but may be a result of the difference in experimental method since the *Cirsium* seeds were planted into the soil rather than scattered on top of it and were consequently less susceptible to predation by small mammals than would otherwise be the case. The better performance of *C. vulgare* in gaps under the 3 cm summer grazing treatment may result from reduced defoliation caused by its more prostrate leaves (Chapter 7 and Appendix 1).

Galium verum was found to outperform *G. aparine* in the absence of winter grazing and also in non-gap treatments, and vice versa. The difference in performance between the species in gap/non-gap treatments is not surprising. *G. aparine* often occurs in disturbed areas and is a common weed of arable fields, unlike *G. verum* which tends to grow in established grasslands subject to grazing or mowing. It therefore seems reasonable to expect that *G. aparine* will perform best in the gap and *G. verum* in the non-gap treatments. Observations made during the course of experimental monitoring suggest that *G. verum* suffered a greater amount of slug damage than *G. aparine* in the gap treatments. *G. verum* has a thinner and smoother stem than *G. aparine*, and it seems possible that it is either more palatable to slugs or more readily killed by them although this suggestion is speculative. In the case of *Silene dioica*, Westerbergh and Nyberg (1995) showed that glabrous plants were preferentially grazed by two slug species (*Arion fasciatus* and *A. subfuscus*) at both the seedling and adult stage.

For all species, the apparent germination recorded in the field was well below that recorded in the laboratory. It is unclear to what extent this reflects poorer germination and/or substantial seed predation and to what extent it reflects the loss of freshly germinated seedlings between monitoring periods. Fenner (1987) argues that seedling loss is often underestimated, but concedes that this is difficult to remedy unless plot monitoring is continuous. For the purposes of this work, however, an absolute measure of seed germination is much less important than a comparative measure between congeners.

Subject to the limitation that the results discussed here only apply to the early stages of growth, they do not support the hypothesis that the five absent species are lacking from the grazing trial because they are intrinsically unsuitable in some way. Each of the absent species performed at least as well as its congener under one or more experimental treatments. The answer to the first question therefore appears to be 'no'. The species which already occur in the grazing trial do not necessarily perform better than their absent congeners. The absence from the grazing trial of five of the species studied here would therefore appear either to result from dispersal limitation (e.g. see Davis *et al.* 1985, Tilman 1997) or from causes which operate at later stages in the life cycle, and I return to this point in Chapter 5.

Treatment effects

Beyond the congeneric differences discussed above and any interaction between species identity and other experimental treatments, what are the effects of the different grazing combinations and gap treatments on species performance?

The effects of the experimental treatments were found to depend very much on the plants under investigation. The effects of grazing proved to be variable, with *Galium verum*, for example, being adversely affected by winter grazing and *G. aparine* benefiting by it. An interaction between summer and winter grazing was observed in the case of *Leontodon hispidus*, with the two levels of summer grazing having almost identical results in the absence of winter grazing, but with high summer grazing pressure leading to poorer

performance in paddocks which also receive winter grazing. The reason for the latter result is not clear, but is presumably due to 'carry over' effects of summer grazing, since the period over which the *Leontodon* experiment took place fell entirely outside the summer grazing period.

In the case of the two *Rumex* species, the only marginally significant experimental effect was recorded for gap treatment, with more individuals of both species germinating and reaching the two true leaf stage in gaps than in the native sward. This is consistent with what is known of their ecology, since both species tend to be particularly prevalent on disturbed ground such as may be found in poorly managed pastures (e.g. Lousley and Kent 1981, Clapham *et al.* 1987). There is good evidence that gaps may be of great importance in allowing species to gain a foothold in a community from which they were previously absent or to become more widespread within a community where they already occur (e.g. Burke and Grime 1996, Bullock *et al.* 1994 and 1995). Gaps were found to be beneficial for *Galium aparine*, both *Cirsium* species and both *Rumex* species in the present study. Wardle *et al.* (1992) found that emergence of seedlings of *Cirsium vulgare* was negatively correlated with pasture cover density, and suggest that in part, adverse effects of plant cover on thistle growth may be due to alleopathic effects as well as the more obvious effects on the light environment. Adverse effects of gaps were, however, recorded for *Galium verum* and *Leontodon hispidus*. This result supports the view that the creation of gaps in a sward may be an important influence on community change, but indicates that not all species are equally favoured and some are adversely affected. The adverse effects observed in the present study may perhaps be due to the drying out of bare soil (an explanation also offered by Panetta and Wardle 1992, in a study of a New Zealand pasture) or the greater ease with which seedlings may be detected by herbivores such as slugs. None of the experimental treatments significantly affected the two *Trifolium* species.

These experiments therefore suggest that species behave individualistically, although their performance in the grazing trial under different experimental conditions can, to some extent, be predicted by knowledge of their ecology.

Chapter 5. Barriers to colonisation from the species pool: the later stages of growth

5.1 Introduction

The experiments described in Chapter 4 relate to the early stages of growth. It is, however, quite conceivable that a plant which has overcome potential barriers to colonisation such as dispersal limitation and germination may succumb to other barriers later in its life cycle which prevent it from becoming established in the community. In this chapter, I compare the survival of the five congeneric pairs examined in Chapter 4 at a later stage in the life cycle, using the same site and grazing treatments as used in the previous chapter.

Differential survival of the congeners is of particular relevance to community assembly, and the field experiments reported in this chapter and the previous one provide information about survival during different stages of growth. Given that the two experiments can (and do, see section 5.3.1) show contrary results with one species of a pair performing best during one stage of growth and the other performing best during a different stage, the question of whether there are any overall differences in performance arises. I attempt to answer this question by also undertaking a combined comparison in which the overall probabilities of survival for the congeneric pairs are analysed.

5.2 Methods

5.2.1 Field experiment

Plants of the five congeneric pairs were grown as plugs in Plantpak P180 trays, filled with John Innes No.1 compost. The seed sources are listed in Chapter 4. The root 'ball' produced in this way takes the form of a steep truncated pyramid, square in section and 3.5 cm deep, with 2.5 cm sides at the top and 1.8 cm at the bottom. Seeds were sown into the plug trays at various dates during 1996 and early 1997 to obtain adequate numbers of congeners at the same stage of development (see below). The plugs were kept out of doors in Milton Keynes until ready for planting into the field experiment. In periods of dry weather the plug trays were watered as required. Variability in germination and constraints on the amounts of seed available resulted in there being unequal numbers of plugs for some pairs of species (Table 5.1).

The plugs were planted into the grazing trial on a pair-wise basis once the plants had reached the stage of development at which the experiments described in the previous chapter were terminated (either two true-leaves or two whorls of leaves). Plugs were planted 20 cm apart (40 cm in the case of *Cirsium*) in two rows 20 cm (or 40 cm in the case of *Cirsium*) apart. The location of the two rows was selected at random with the constraint that other experimental plots and a 10 m border around the paddock edges were avoided. The position of the plots was marked using wooden pegs, and the arrangement of the plugs in the two rows was randomised. A core of soil similar in size to the plugs being planted was extracted by hammering a sharp metal tube into the ground and removing it together

with a plug-sized core of soil. The plug was then inserted into the hole, pushed firmly into the ground and watered in. Plugs were watered as required during the first month of establishment. The progress of the plugs was monitored initially on approximately a fortnightly basis and subsequently once every one or two months. Positions of the plugs were relocated by stretching a tape between the wooden pegs marking the ends of the plots. For the purposes of this chapter, I have undertaken a series of congeneric analyses and simply compare the proportion of plugs of each species surviving to a particular time with the proportion of surviving plugs of its congener under the four grazing treatment combinations. Some species (e.g. both *Rumex* spp.) showed a slower decline in numbers than others (e.g. *Galium aparine*), and some species are annuals whilst others are biennials or perennials. These facts dictate that the different experiments should be examined over a period of time suited to each congeneric pair. The procedure adopted here has been to examine the data from that monitoring visit at which approximately half the total number of planted congeners was still alive, subject to the following constraint. In cases where one of the congeners is an annual species, the analysis was performed on data gathered before any individuals of the annual had died following completion of the life cycle (flowering and seed set). This was considered to be a good compromise between retaining a sufficiently large sample size whilst allowing adequate time for the treatments to take effect. In the event, for three of the five congeneric pairs the data used in the analysis presented here were recorded on 13 March 1997. The numbers of plugs planted, dates of planting and recording (for the purposes of the analysis described here) are shown in Table 5.1.

Species	Number planted per paddock	Date planted	Date recorded
Galium aparine & *G. verum*	40 40	25 March 1996	6 June 1996
Trifolium pratense & *T. dubium*	45 45	21 April 1997	3 July 1997
Rumex crispus & *R. obtusifolius*	40 40	24 April 1996	13 March 1997
Cirsium vulgare & *C. eriophorum*	15 41 (Block1), 29 (Block2)	3 July 1996	13 March 1997
Leontodon autumnalis & *L. hispidus*	15 45	6 July 1996	13 March 1997

Table 5.1. Congeneric pairs: numbers of plugs planted per paddock, date of plug planting and recording date.

5.2.2 Statistical analysis of the field experiment

For the purposes of this experiment, I have analysed the proportion of plants surviving at a particular time. The experiment is a factorial 2x2x2 (winter x summer x species) split plot design with two replicates of each treatment combination. In circumstances such as this when the proportions being analysed are all near to 0.5, a standard ANOVA may be a suitable (if approximate) method of analysis (Dyke and Patterson 1952). When this is not the case, arcsine transformation is commonly applied to the proportional data, after which a standard ANOVA is undertaken. Arcsine transformation only yields a valid analysis, however, when there are equal numbers of units in each class. If this is not the case, the transformed values have unequal variance and one of the fundamental ANOVA assumptions is violated. Two of the five experiments undertaken here have unequal class sizes due to limited amounts of experimental material being available (e.g. only 15 plants of *Leontodon autumnalis* being planted per paddock compared with 45 plants of *L. hispidus*). For this reason, analysis took the form of fitting a generalized linear model with logit link function (see Dobson 1990 and McCullagh and Nelder 1989 for a discussion of these models). Statistical significance was assessed by an analysis of deviance table (which is broadly similar to an analysis of variance table, except that the deviance rather than sums of squares is partitioned between the various model terms). The terms were removed from the full

model one by one, with the resulting change in deviance being tested against the chi-squared distribution on one degree of freedom.

5.2.3 A combined analysis

The data in the first series of field experiments (Chapter 4) were analysed as the number of plants germinating or surviving, since this yielded the simplest analysis of a somewhat complicated set of experiments. By contrast, the data from the experiments described in this chapter were of necessity analysed as proportions since the number of individuals present at the start of the experiments was different for some congeneric pairs. The data from the first set of experiments can, however, be used to estimate the proportion of individuals of a species (and hence probability of a plant chosen at random) surviving to the two true-leaf stage simply by dividing the number of survivors at the two true-leaf stage by the number of seeds initially sown. The second set of experiments follows plant survival from the growth stage at which the first experiment was terminated, and the two survival probabilities produced by the two experiments (here termed P_1 and P_2) may therefore be multiplied together to obtain an estimate of the overall probability (or compound probability, here termed P_{comp}) of survival from seed planting to the termination of the second set of experiments. It is very relevant to community assembly to ask whether there are overall differences in survival probability between congeners. The results must be interpreted with caution (see section 5.4), but to the extent that the two sets of field experiments enable comparisons to be made, I have adopted the following procedure.

For each congeneric pair, survival probabilities for the two experiments have been calculated as described above. Where either experiment suggested that the performance of congeners relative to one another may vary according to experimental treatment (i.e. a significant species x treatment interaction was observed), survival probabilities and

subsequent analysis were undertaken for the relevant treatment combinations separately. The overall survival probabilities P_{comp} were compared for congeners by calculating the ratio (here termed the 'P ratio') of P_{comp} for the species naturally present in the grazing trial divided by P_{comp} for the species not naturally present. Thus a ratio greater than one indicates that, over the course of the experiments, the species naturally present outperforms its absent congener. A ratio less than one indicates the reverse. The statistical significance of any departures from unity has been assessed using the randomisation method of bootstrapping (Manly 1991). The true survival probabilities for each congener in each analysis are taken as unknown, but are estimated as the observed values P_1 and P_2. These probabilities are then in effect used to 'recreate' the data from which they were obtained. If, for example, P_1 is estimated as 0.3 from a sample size of 800 seeds and P_2 estimated as 0.5 from a sample size of 120 plugs, then two samples are randomly drawn from binomial distributions with p=0.3, n=800 and p=0.5, n=120 respectively. The P_1, P_2 and P_{comp} values are then obtained from the randomisation and the same procedure undertaken for the congener after which the P ratio is calculated. For all analyses this procedure has been repeated 10,000 times and the distribution of the P ratio obtained. The significance of the departures from the hypothesised value of one has been assessed against the randomisations.

In cases where the differences between congeners were investigated separately for different gap treatments, the same P_2 values were used for each species because the effect of gaps was only investigated in the first experiment.

5.3 Results

5.3.1 Results I: field experiment

5.3.1.1 *Galium*

The results of the *Galium* plug experiment are shown at Table 5.2. The effects of species and winter grazing were significant in the form of an interaction as well as main effects. *G. verum* outperformed *G. aparine* under all conditions, and winter grazing improved the performance of both species but led to a slightly greater improvement in the case of *G. verum* (winter ungrazed: 43.1% survival for *G. aparine vs.* 68.1% for *G. verum*; winter grazed: 59.4% survival for *G. aparine vs.* 93.8% for *G. verum*). The interaction is shown graphically at Figure 5.1.

Term	Deviance associated with term	Significance
Winter (W)	31.69	**p=0.0000**
Summer (S)	1.65	p=0.1989
Species (Sp)	68.36	**p=0.0000**
Block	2.38	p=0.1228
WxS	1.89	p=0.1697
WxSp	9.61	**p=0.0019**
SxSp	2.71	p=0.0999
WxSxSp	0.07	p=0.7887

Table 5.2. *Galium* plug experiment. The deviance is partitioned between the different terms and their significance (see column 3) assessed against the chi-squared distribution. Bonferroni corrected 5% cut-off point at p=0.0064.

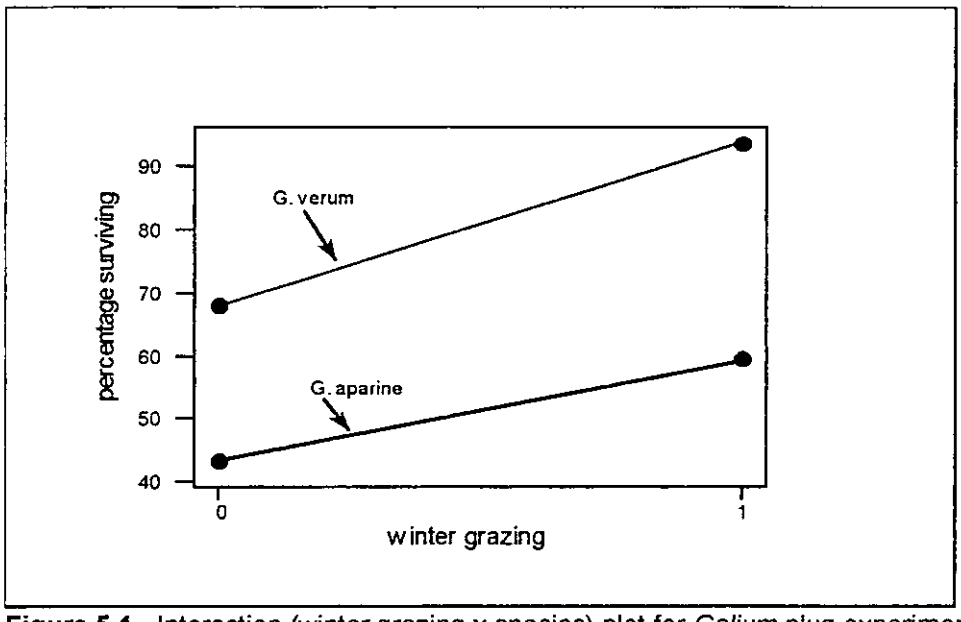


Figure 5.1. Interaction (winter grazing x species) plot for *Galium* plug experiment.

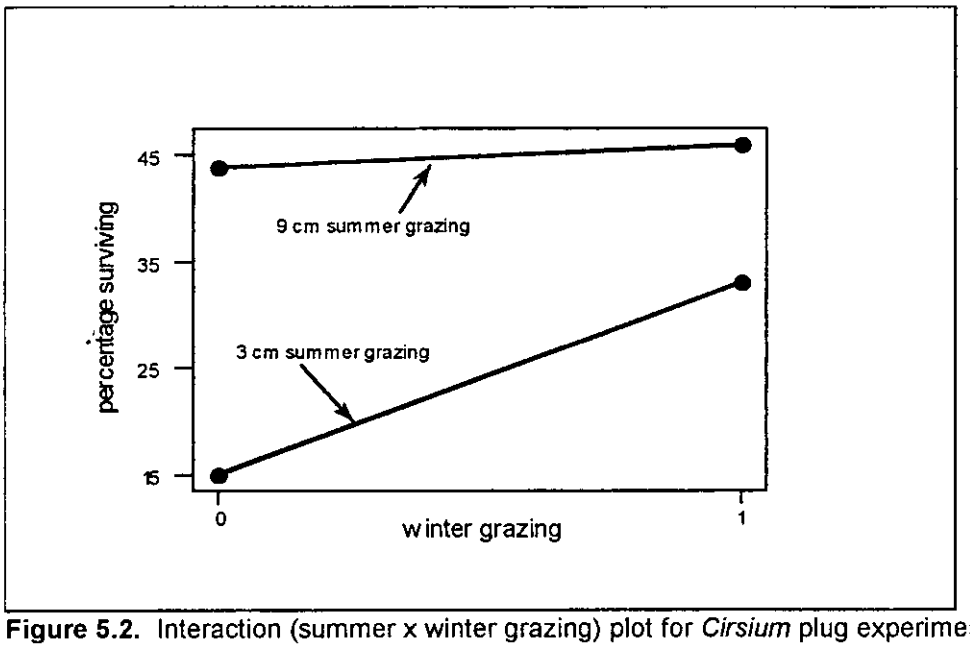


Figure 5.2. Interaction (summer x winter grazing) plot for *Cirsium* plug experiment.

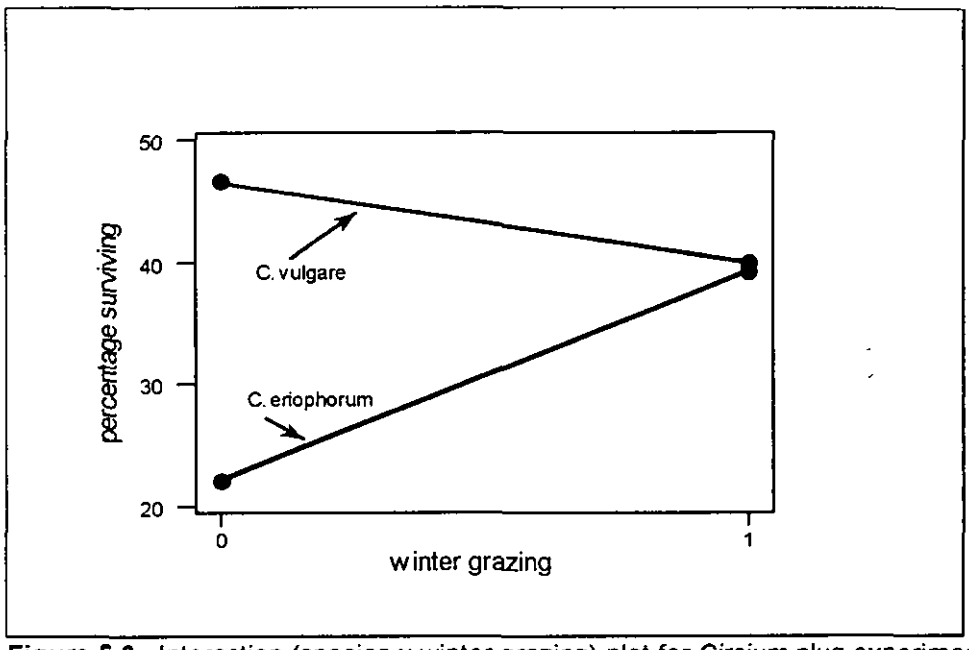


Figure 5.3. Interaction (species x winter grazing) plot for *Cirsium* plug experiment.

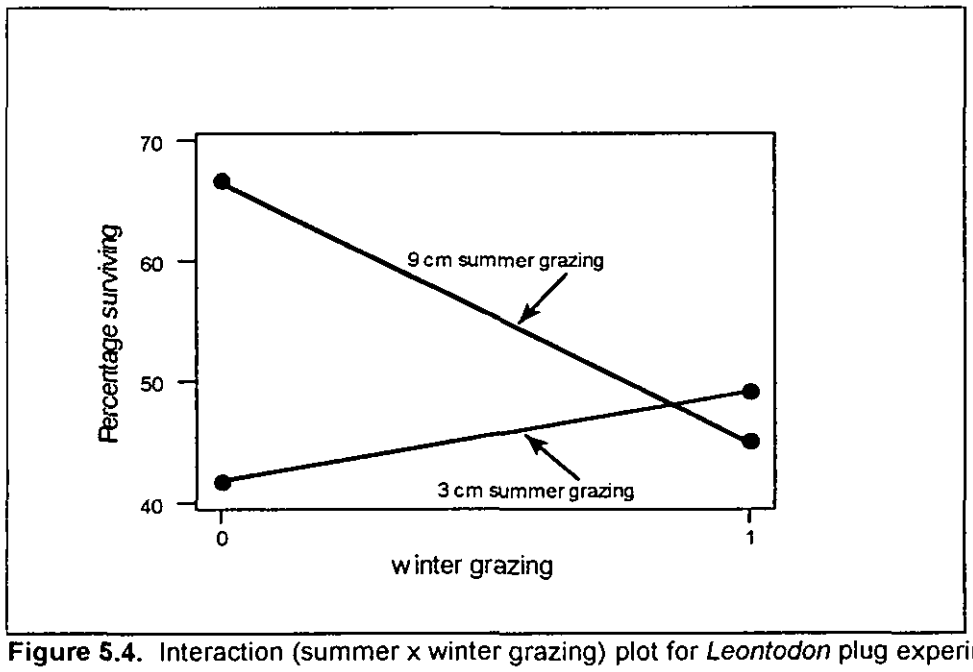


Figure 5.4. Interaction (summer x winter grazing) plot for *Leontodon* plug experiment.

5.3.1.2 *Trifolium*

The results of the *Trifolium* plug experiment are shown at Table 5.3. Three significant or marginal main effects were recorded. Under winter grazing, plants showed better survival compared with the ungrazed treatment (76.4% *vs.* 63.1% respectively). Summer grazing to 9 cm improved survival compared with 3 cm grazing (73.1% *vs.* 66.4% respectively), and a significant species effect was recorded, with *T. pratense* showing better survival than *T. dubium* (75.6% *vs.* 63.9% respectively).

Term	Deviance associated with term	Significance
Winter (W)	15.25	**p=0.0001**
Summer (S)	3.88	***p=0.0489***
Species (Sp)	11.98	**p=0.0005**
Block	1.35	p=0.2456
WxS	0.01	p=0.9324
WxSp	3.61	p=0.0573
SxSp	2.31	p=0.1282
WxSxSp	0.36	p=0.5499

Table 5.3. *Trifolium* plug experiment. The deviance is partitioned between the different terms and their significance (see column 3) assessed against the chi-squared distribution. Bonferroni corrected 5% cut-off point at p=0.0064.

5.3.1.3 *Rumex*

The results of the *Rumex* plug experiment are shown at Table 5.4. Three significant or marginal main effects were recorded. Summer grazing to 9 cm improved survival compared with 3 cm grazing (64.7% *vs.* 56.3% respectively). A greater proportion of plugs survived in Block 1 compared with Block 2 (70.3% *vs.* 50.6% respectively), and a species effect was recorded with *R. crispus* outperforming *R. obtusifolius* (68.8% survival *vs.* 52.2% respectively).

Term	Deviance associated with term	Significance
Winter (W)	0.79	p=0.3738
Summer (S)	4.78	***p=0.0288***
Species (Sp)	18.63	**p=0.0000**
Block	27.21	**p=0.0000**
WxS	0.39	p=0.5338
WxSp	0.71	p=0.3978
SxSp	3.20	p=0.0737
WxSxSp	0.05	p=0.8164

Table 5.4. *Rumex* plug experiment. The deviance is partitioned between the different terms and their significance (see column 3) assessed against the chi-squared distribution. Bonferroni corrected 5% cut-off point at p=0.0064.

5.3.1.4 *Cirsium*

The results of the *Cirsium* plug experiment are shown at Table 5.5. Significant or marginal winter and summer grazing effects were recorded in the form of an interaction as well as main effects. Winter grazing showed little effect following a 9 cm summer grazing regime (44.0% survival, winter ungrazed *vs.* 46.0% survival, winter grazed) but showed differing effects after a 3 cm summer grazing regime (15.0% survival, winter ungrazed *vs.* 33% survival, winter grazed). A marginal species effect in the form of an interaction with winter grazing as well as a main effect was observed (*C. eriophorum* 22.1% survival, winter ungrazed *vs.* 39.3% survival, winter grazed; *C. vulgare* 46.7% survival winter ungrazed *vs.* 40% survival, winter grazed). The interactions are shown graphically at Figures 5.2 and 5.3.

Term	Deviance associated with term	Significance
Winter (W)	4.44	***p=0.0352***
Summer (S)	19.98	**p=0.0000**
Species (Sp)	6.20	***p=0.0128***
Block	1.55	p=0.2126
WxS	4.53	***p=0.0332***
WxSp	6.96	***p=0.0084***
SxSp	0.10	p=0.7494
WxSxSp	0.17	p=0.6816

Table 5.5. *Cirsium* plug experiment. The deviance is partitioned between the different terms and their significance (see column 3) assessed against the chi-squared distribution. Bonferroni corrected 5% cut-off point at p=0.0064.

5.3.1.5 *Leontodon*

The results of the *Leontodon* grazing experiment are shown at Table 5.6. A significantly greater proportion of plugs survived in Block 1 compared with Block 2 (63.8% *vs.* 37.5% respectively). Summer grazing showed a marginal main effect and as a term in a significant interaction with winter grazing (when summer grazed to 9 cm: 66.7% survival, winter ungrazed *vs.* 45% survival, winter grazed; when summer grazed to 3 cm: 41.7% survival, winter ungrazed *vs.* 49.2% survival, winter grazed). This interaction is shown graphically at Figure 5.4.

Term	Deviance associated with term	Significance
Winter (W)	2.41	p=0.1205
Summer (S)	5.25	***p=0.0220***
Species (Sp)	3.08	p=0.0790
Block	34.28	**p=0.0000**
WxS	11.32	**p=0.0008**
WxSp	2.44	p=0.1180
SxSp	0.53	p=0.4654
WxSxSp	0.15	p=0.6944

Table 5.6. *Leontodon* plug experiment. The deviance is partitioned between the different terms and their significance (see column 3) assessed against the chi-squared distribution. Bonferroni corrected 5% cut-off point at p=0.0064. See text for more details.

5.3.2 Results II: combined analysis

5.3.2.1 *Galium*

The two *Galium* experiments revealed interactions of species with winter grazing and gap treatment. When considered overall, *Galium verum* (the 'absent' congener) outperformed *G. aparine* in three out of the four comparisons, and in two cases the difference was statistically significant (Table 5.7). *G. aparine* showed a slightly better overall performance in the presence of winter grazing than *G. verum*, but this was statistically insignificant.

Species	Treatment	P_1	P_2	P_{comp}	*P* ratio	Significance
G. aparine	Winter grazing = 0	0.1438	0.4313	0.0620	**0.3279**	p<<**0.0001**
G. verum		0.2775	0.6813	0.1890		
G. aparine	Winter grazing = 1	0.2250	0.5938	0.1336	1.0270	p=0.4054
G. verum		0.1388	0.9375	0.1301		
G. aparine	Gap = 0	0.1438	0.5125	0.0737	**0.3605**	p<<**0.0001**
G. verum		0.2525	0.8094	0.2044		
G. aparine	Gap = 1	0.2250	0.5125	0.1153	0.8701	p=0.1022
G. verum		0.1638	0.8094	0.1325		

Table 5.7. Overall survival of the *Galium* species over the course of the two experiments. The congeneric comparison is made separately over four different experimental treatments (second column). The probability of survival over the course of the first (Chapter 4) experiment is given in column 3, and the probability of survival over the second (Chapter 5) experiment is given in column 4. The compound probability (P_1 x P_2) is given in column 5, and the ratio of the compound probability of *G. aparine/G. verum* is given in column 6. Statistical significance is given in column 7. Bonferroni corrected 5% cut-off point at p=0.0127.

5.3.2.2 *Trifolium*

The *Trifolium* data were pooled over the entire experiment. *Trifolium dubium* (the 'absent' congener) performed very significantly better overall than *T. pratense* (Table 5.8).

Species	P_1	P_2	P_{comp}	*P* ratio	Significance
T. pratense	0.0013	0.7556	0.0009	**0.0438**	p<<**0.0001**
T. dubium	0.0338	0.6386	0.0216		

Table 5.8. Overall survival of the *Trifolium* species over the course of the two experiments. The congeneric comparison is averaged over all experimental treatments. The probability of survival over the course of the first (Chapter 4) experiment is given in column 2, and the probability of survival over the second (Chapter 5) experiment is given in column 3. The compound probability (P_1 x P_2) is given in column 4, and the ratio of the compound probability of *T. pratense /T. dubium* is given in column 5. Statistical significance is given in column 6.

5.3.2.3 *Rumex*

The results of the *Rumex* comparison are shown separately for the two summer grazing treatments at Table 5.9. In both cases, *R. crispus* (the naturally present congener) performed either marginally or significantly better overall than *R. obtusifolius*.

Species	Treatment	P_1	P_2	P_{comp}	P ratio	Significance
R. crispus	Summer grazing = 3cm	0.0550	0.6813	0.0375	**1.7776**	p=**0.0007**
R. obtusifolius		0.0475	0.4438	0.0211		
R. crispus	Summer grazing = 9cm	0.0538	0.6938	0.0373	**1.3811**	***p=0.0355***
R. obtusifolius		0.0450	0.6000	0.0270		

Table 5.9. Overall survival of the *Rumex* species over the course of the two experiments. The congeneric comparison is made separately over two different experimental treatments (second column). The probability of survival over the course of the first (Chapter 4) experiment is given in column 3, and the probability of survival over the second (Chapter 5) experiment is given in column 4. The compound probability (P_1 x P_2) is given in column 5, and the ratio of the compound probability of *R. crispus/R. obtusifolius* is given in column 6. Bonferroni corrected 5% cut-off point at p=0.0253.

5.3.2.4 *Cirsium*

The *Cirsium* congeners showed a complex three way interaction with summer grazing and gap treatments in the first experiment (Chapter 4), and also an interaction with winter grazing in the plug experiment. The overall performance is therefore compared for six separate treatment combinations in Table 5.10. *C. eriophorum* showed a significantly (or, in one case, marginally) better overall performance than *C. vulgare*.

Species	Treatment	P_1	P_2	P_{comp}	P ratio	Significance
C. vulgare	Summer grazing = 3cm	0.1140	0.3000	0.0342	**0.2179**	p<<**0.0001**
C. eriophorum	Gap = 0	0.7565	0.2075	0.1570		
C. vulgare	Summer grazing = 3cm	0.3270	0.3000	0.0981	**0.5490**	***p= 0.0113***
C. eriophorum	Gap = 1	0.8612	0.2075	0.1787		
C. vulgare	Summer grazing = 9cm	0.1325	0.5500	0.0729	**0.3430**	p<<**0.0001**
C. eriophorum	Gap = 0	0.5220	0.4070	0.2125		
C. vulgare	Summer grazing = 9cm	0.3490	0.5500	0.1920	**0.5790**	p=**0.0007**
C. eriophorum	Gap = 1	0.8145	0.4070	0.3315		
C. vulgare	Winter grazing = 0	0.2035	0.4667	0.0950	**0.5230**	p=**0.0026**
C. eriophorum		0.8196	0.2215	0.1815		
C. vulgare	Winter grazing = 1	0.2578	0.3833	0.0988	**0.3824**	p<<**0.0001**
C. eriophorum		0.6575	0.3930	0.2584		

Table 5.10. Overall survival of the *Cirsium* species over the course of the two experiments. The congeneric comparison is made separately over six different experimental treatments or treatment combinations (second column). The probability of survival over the course of the first (Chapter 4) experiment is given in column 3, and the probability of survival over the second (Chapter 5) experiment is given in column 4. The compound probability (P_1 x P_2) is given in column 5, and the ratio of the compound probability of *C. vulgare/C. eriophorum* is given in column 6. Statistical significance is given in column 7. Bonferroni corrected 5% cut-off point at p=0.0085

5.3.2.5 *Leontodon*

The overall difference in performance for the *Leontodon* congeners is given at Table 5.11. The first experiment (Chapter 4) showed several significant interactions between species

and other experimental treatments but, as argued there, this is a result of the very poor viability of the *L. autumnalis* seed. Table 5.11 simply compares the two species. In the absence of any field germination of *L. autumnalis*, it is not surprising that Table 5.11 shows a very significantly better performance on the part of *L. hispidus*, but this result is shown here for the sake of completeness. The conclusion remains unaltered if the value of P_1 for *L. autumnalis* is replaced by 0.02, the laboratory germination probability obtained under light treatment.

Species	P_1	P_2	P_{comp}	*P* ratio	Significance
L. autumnalis	0.0000	0.5750	0.0000	**0.0000**	$p<<0.0001$
L. hispidus	0.1438	0.4833	0.0695		

Table 5.11. Overall survival of the *Leontodon* species over the course of the two experiments. The congeneric comparison is averaged over all experimental treatments. The probability of survival over the course of the first (Chapter 4) experiment is given in column 2, and the probability of survival over the second (Chapter 5) experiment is given in column 3. The compound probability (P_1 x P_2) is given in column 4, and the ratio of the compound probability of *L. autumnalis* /*L. hispidus* is given in column 5. Statistical significance is given in column 6.

5.4 Discussion

The two questions being examined by the experiments in this chapter are the same as those posed in Chapter 4: *i)* do the species naturally present in the grazing trial perform better than those which are not?, *ii)* what effects do the different combinations of management have on plant performance, and are different species affected in the same way? In addition I compare overall plant performance, quantified as survival probability over the course of the field experiments. These three matters are discussed separately below.

Comparison of plug performance between congeners

Species effects were observed for all congeneric pairs except for *Leontodon*, although interactions with grazing rather than straightforward main effects were present in two cases. *Rumex crispus* (the species already present in the grazing trial) outperformed *R. obtusifolius*, in contrast with the field germination results reported in Chapter 4. The reason for the better performance of *R. crispus* plugs is not clear, and a study of the niche

requirements of the two *Rumex* species in the field (see Chapter 6) failed to detect any important differences between them. The result is, however, in agreement with the findings of Hongo (1989) who monitored transplants of these two *Rumex* species over a four year period. *Trifolium pratense* (already present in the grazing trial) outperformed *T. dubium*, again in contrast with performance during the early stages of growth reported in Chapter 4. The reason for this is also not clear, since both species do occur in grazed situations and appear to show a reasonable degree of niche overlap (Chapter 6). Neither appears to be markedly better suited to conditions in the grazing trial than the other, with the exception of the differences reported in Chapter 4 attributed to seed predation.

Species effects in *Galium* and *Cirsium* were more complex, with interactions between species identity and grazing treatment being observed. *Galium verum* (naturally absent from the grazing trial) outperformed *G. aparine* under all experimental conditions, but species identity showed an interaction with winter grazing such that *G. verum* benefited slightly more from winter grazing than did *G. aparine*. Field observations (see Chapter 6) suggest that *G. verum* occurs frequently as a member of grazed grassland communities whilst *G. aparine* tends to occur more in rank grassland, infrequently cut or grazed.

In the case of *Cirsium*, a species x winter grazing interaction was again noted. In this case, *C. vulgare* (already present in the grazing trial) outperformed *C. eriophorum* under all treatment combinations, but a large difference in species performance was observed in the absence of winter grazing whilst only a negligible difference was observed in the presence of winter grazing. *C. eriophorum* shows a lower growth rate than *C. vulgare* during the early stages of growth (Chapter 7) and in the absence of winter grazing, perhaps *C. eriophorum* suffers disproportionately through competition from the surrounding vegetation. The better performance of *C. vulgare* plugs in the grazing trial compared with

C. eriophorum is consistent with the apparently broader niche occupancy of *C. vulgare* suggested in Chapter 6, in which *C. vulgare* appears to be somewhat better suited to conditions such as those prevailing at the grazing trial.

Effects of different grazing treatments

Straightforward main effects of summer grazing were observed in the *Rumex* and *Trifolium* experiments, and in both cases the results were the same. Summer grazing to a sward height of 3 cm had an adverse effect on plants compared with a 9 cm summer sward height. This effect is presumably due directly to herbivory, with heavily grazed plants suffering a higher mortality than those which are more lightly grazed.

In the *Galium* experiment, winter grazing had an effect via an interaction with species identity as discussed above. The plugs were planted at the very end of the winter grazing season, and the effect of winter grazing seems most likely to be an indirect one mediated perhaps by the structure of the sward rather than the direct effect of grazing on the plugs. Similarly, the beneficial effect of winter grazing effect on *Trifolium* must be an indirect one since the plugs were planted and monitored outside the winter season. A winter x summer grazing interaction was observed in both the *Leontodon* and *Cirsium* experiments. In the case of *Leontodon*, winter grazing was seen to have an adverse effect following a 9 cm summer grazing regime, but a beneficial effect after a 3 cm summer grazing regime. In the case of *Cirsium* the interaction was slightly different. Winter grazing produced little effect after a 9 cm summer grazing regime in contrast with the results for *Leontodon*, but again had a beneficial effect following a 3 cm summer grazing regime. I am unable to offer a convincing explanation for either of these interactions.

Comparison between experiments and overall performance between congeners

The field experiments described in this chapter are short-term in comparison with the potential life-span of most of the species considered here, since even "biennial" plants may show a pre-reproductive period of over seven years (e.g. Klinkhamer *et al.* 1996). In addition, two of the five comparisons are between annual and perennial species and when comparing species with different life histories, it is impossible to gain a full idea of their relative performance without following both species through the complete life cycle. Such an endeavour would require many years of study for most of the species examined here, and is clearly beyond the scope of a project such as this. Conclusions about long-term effects on community composition must therefore be tentatively drawn. Despite this caveat, the question of whether the species which are naturally found in the grazing trial tend to perform better, worse or no differently from their absent congeners is an interesting and relevant one which is worth pursuing as far as possible.

Comparison of the survival probabilities in Tables 5.7-5.11 suggests that performance in the early stages of growth (germination to two true leaves or leaf whorls) is no indication of performance later on. Comparing the two sets of experiments separately, in the *Rumex*, *Trifolium* and *Cirsium* experiments, the field germination results ran contrary to those of the plug study. In each case, the species which was naturally absent from the grazing trial usually (in the case of *Cirsium*) or invariably (*Rumex* and *Trifolium*) performed better than its congener at the germination stage but worse during the later stages of growth. The *Leontodon* experiment is harder to draw conclusions from because of the poor germination of *L. autumnalis*, although no difference in species performance was noted in the later stages of growth. The *Galium* experiments both revealed interactions which prevent simple conclusions being drawn, but under at least some treatments, the naturally absent species (*G. verum*) might be expected to grow satisfactorily in the grazing trial.

With regard to the overall performance of the congeners, most significant departures from randomness related to the absent species outperforming its native congener. Despite the caveats mentioned above, the fact remains that the species naturally present in the grazing trial show no general and overwhelming evidence that they outperform absent congeners. Only in the *Rumex* comparison did the species native to the sward outperform the 'introduced' species. The model developed in Chapter 3 suggests that both species have an approximately equal probability of occurring in the grazing trial (a probability of 0.69 for *R. crispus* compared with 0.71 for *R. obtusifolius*).

In the case of the *Trifolium* experiment, *T. dubium* (naturally absent from the grazing trial) performed much better than *T. pratense* during the first experiment. Although it performed worse during the plug experiment, it showed a significantly better overall performance and a number of individuals survived to flower and set seed. The evidence therefore suggests that *T. dubium* would also be able to grow and perhaps maintain populations in the grazing trial in the absence of dispersal limitation, even if a longer term experiment were to show that *T. pratense* exhibits a comparable or better overall performance. The model developed in Chapter 3 suggests both species have an approximately equal probability of occurring in the site (0.75 for *T. dubium* compared with 0.72 for *T. pratense*). Similar comments might be made about *Galium* and *Cirsium*, although in the latter case *C. eriophorum* (the absent congener) was outperformed by *C. vulgare* in the plug experiment and it is possible that the overall performance of *C. vulgare* might be greater than *C. eriophorum* if the experiment was run over the course of the life cycle of these species. The model developed in Chapter 3 suggests that the two Galium species have an approximately equal probability of occurring in the site (0.61 for *G. verum* compared with 0.65 for *G. aparine*) but that there is a large difference between the probabilities for the two thistle species (0.16 for *C.*

eriophorum compared with 0.68 for *C. vulgare*). The overall results of the *Leontodon* experiments reflect the very poor germination of *L. autumnalis* seed. As argued in Chapter 4, there is no reason to suppose that such poor germination is typical of the species, but the fact remains that *L. hispidus* performed reasonably well (showing similar overall survival to *C. vulgare*, also in the Asteraceae, under several treatments over a similar period of time), and the evidence suggests that *L. hispidus* might be able to maintain viable populations following initial establishment. The model developed in Chapter 3 suggests that *L. hispidus* is marginally more likely to occur in the grazing trial (a probability of 0.65 for *L. hispidus* compared with 0.60 for *L. autumnalis*). Such results suggest that communities bear the strong imprint of dispersal limitation as has been argued by other authors (e.g. Tilman 1997, Primack and Miao 1992). If this is the case, then predicting community composition will require us to model dispersal into the community as well as subsequent establishment. This is a highly problematic matter, and one returned to in Chapter 8.

Although limited to ten species and not examining the complete life cycle in most cases, the results reported in this chapter are consistent with the view of the species pool and realised community discussed in Chapter 3. Species other than those already there may be able to establish themselves in a community, and a full investigation of community assembly should recognise that an actual community may be only one of the many possible.

Chapter 6. Niche occupancy for the ten study species: using associated vegetation as a niche bioassay

6.1 Introduction

In the two previous chapters I describe experimental studies on ten selected species. The advantage of doing experiments is that one can to a large extent control the factors of interest, and explore their effects in the absence of confounding influences. There is, however, the problem of deciding exactly how the findings of the experimental work relate to what happens in nature. Can we be sure that planted species respond to environmental influences in the same way as those which have grown naturally? Or do they perform similarly in artificial and natural gaps? The most robust approach is to investigate ecological problems in different ways and to see if the results are consilient. In parallel with the experimental studies described in Chapters 4 and 5, an observational study was therefore undertaken. The objective of this was to learn more about the ecology of the five pairs of species by studying them in communities at other sites. Can this information assist in interpreting the experimental results obtained from the grazing trial? In particular, I wish to discover if there is evidence of niche differentiation within the five pairs of study species, and if so, whether the species which is present in the grazing trial is more typical of this kind of community than the absent congener.

The niche occupied by a plant is difficult to measure with any certainty. It comprises the 'volume' occupied by a plant in a multivariate space of indefinitely many dimensions, with the axes representing various biotic and abiotic factors. Which are the ones which are important in defining the niche for a particular species? Attempts have been made to quantify plant niche differences on the basis of some easily measured variables such as amount of leaf litter, slope and aspect, for example using discriminant analysis (Mann and Shugart 1983). For the present study, the measurement of such factors was considered impracticable, and an alternative method was sought. I have therefore used plants themselves as descriptors of 'niche' or, put another way, as a niche bioassay (Prentice and Cramer 1990).

Ecologists have long been aware that a gradient in some environmental factor may be reflected by a gradient in plant community composition. Well known examples include the distribution of the three buttercup species *Ranunculus repens*, *R. acris* and *R. bulbosus* along the moisture gradient found in ridge and furrow meadows, running from wet to dry respectively. Cody (1978) investigated niche position and niche shifts on mountain foothills for species of *Haplopappus* and *Chrysothamnus*. The responses of various plants have been experimentally investigated along different kinds of gradient and found to differ (e.g. Wedin and Tilman 1993; Rabinowitz *et al.* 1989; Kitajima and Tilman 1996). Even between very similar taxa such as dandelion microspecies (*Taraxacum* spp.), differences in ecological amplitude have been found (Sterk *et al.* 1983) and it is therefore no surprise that the small-scale (quadrat-sized) species composition of a plant community can reflect the complex of biotic and abiotic factors prevailing at that location in a sensitive and accurate way.

The idea behind my approach is a simple one. Data are obtained for quadrats centred on the study species at several sites. For each congeneric pair, an ordination is performed on the quadrat data for the associated species (i.e. data for the 'target' species are not taken into account). The extent of niche-overlap or separation is then judged directly from the ordination diagram. This can be related to the niches 'on offer' at the study site by superimposing on the ordination diagram equivalent quadrat data for the grazing trial.

Information on the full range of niche occupancy for each species would be valuable for the purposes of this study but would involve vast amounts of fieldwork. Instead, I investigate variation in niche occupancy in a pair-wise manner across a limited number of sites as described below.

6.2 Methods

The following procedure was adopted as the best practicable method given the constraints of time. Quadrat data were obtained for all 5 pairs of the study species from a variety of sites in southern and central Britain (Table 6.1). All sites supported neutral to basic grassland and were selected on the basis of either personal knowledge or a study of the appropriate county flora. Each site was initially walked to determine the extent of suitable plant communities and then a systematic search was made for the study species. When one of the study species was located, a 1x1 m (or, in the case of *Cirsium*, a 2x2 m) quadrat was centred on it and the cover of all the vascular plants was recorded on the DOMIN scale. Up to three quadrats per species were recorded for each site, subject to the constraint that they were at least 10 m distant from one another. Once quadrats had been recorded for one species, every effort was made to locate populations of the congener in order that a within

site comparison might be made. Every species was studied in between four and ten separate sites in order to minimise undue influence from any atypical sites.

It is possible to use the DOMIN scores of the associated species as raw data in an ordination. This was the approach initially adopted here, but the following two problems were encountered. Firstly, a very large number of associated species was recorded, and the spatial relationships between the quadrats in this many-dimensioned multivariate space were severely distorted when plotted in two dimensions. Secondly, the axes of the ordination diagrams were not easy to interpret ecologically. Instead, and adopting an approach based on Hawkes *et al.* 1997, for each quadrat an overall value for each of the C, S and R scores (Grime *et al.* 1988) and the Ellenberg numbers for soil moisture (F), soil reaction (R) and soil nutrient level (N) was calculated (see Chapter 3 for information about these values), weighted by the DOMIN score of each species but ignoring the target species. This procedure in effect uses trait values from associated species to obtain information about the environment around each of the target species.

For each pair of congeners, principal components analysis was performed on the six scores for each quadrat, and the position of the quadrats plotted in the first two dimensions of ordination space. In addition to this, a mean C,S and R score and Ellenberg F,R and N-value was also calculated for each paddock using the 1995 quadrat survey data described in Chapter 2. The position of the paddocks was then plotted onto the ordination diagram using the weightings of each of the six variables on the first two principal components. The data from the paddocks therefore play no part in the actual principal components analysis, but are simply superimposed on the final ordination plot. The reason for not including the grazing trial data in the ordinations was that it tended to obscure the feature of primary interest - the extent of niche overlap between congeners.

Species	Site
Cirsium vulgare	Aston Upthorpe, Berks. SU5483 Knap Hill, Wilts. SU1263 Cherhill Down, Wilts. SU0569 Cam Long Down, Glos. ST7799 Crickley Hill, Glos. SO9316 Winstone, Glos. SO9709 Farmoor, Oxon. SP4607 Hassop Mines, Derbys. SK2273 Ousel Meadows, Bucks. SP8937
Cirsium eriophorum	Sharnbrook, Beds. TL0060 Aston Upthorpe, Berks. SU5483 Aston Tyrold, Berks. SU5585 Knap Hill, Wilts. SU1263 Cherhill Down, Wilts. SU0569 Cam Long Down, Glos. ST7799 Crickley Hill, Glos. SO9316 Winstone, Glos. SO9709 Farmoor, Oxon. SP4607 Hassop Mines, Derbys. SK2273
Galium aparine	Ousel Valley, Bucks. SP8937 Little Wittenham, Oxon. SU5692 Upthorpe Downs, Berks. SU5482 Aston Upthorpe, Berks. SU5483 Feltwell, Norfolk. TL7091
Galium verum	Ousel Valley, Bucks. SP8937 Little Wittenham, Oxon. SU5692 Upthorpe Downs, Berks. SU5482 Aston Upthorpe, Berks. SU5483 Feltwell, Norfolk. TL7091
Leontodon autumnalis	Ousel Valley, Bucks. SP8937 W. of Burford, Oxon. SO2312 N. of Burford, Oxon. SO2715 Little Wittenham, Oxon. SU5692 Cherhill Down, Wilts. SU0469 Avebury, Wilts. SU1069
Leontodon hispidus	Aston Upthorpe, Berks. SU5482 Foulden Common, Norfolk. TL7699 Cranwich, Norfolk. TL7692 Feltwell, Norfolk. TL7091 Little Wittenham, Oxon. SU5692 Cherhill Down, Wilts. SU0469 Avebury, Wilts. SU1069
Rumex crispus	Chulmleigh, Devon. SS6914 Ousel Valley, Bucks. SP8937 Weeting, Norfolk. TL7589 Feltwell, Norfolk. TL7091 Little Wittenham, Oxon. SU5692
Rumex obtusifolius	Chulmleigh, Devon. SS6914 Ousel Valley, Bucks. SP8937 Weeting, Norfolk. TL7589 Feltwell, Norfolk. TL7091 Little Wittenham, Oxon. SU5692
Trifolium pratense	Ousel Valley, Bucks. SP8937 Little Wittenham, Oxon. SU5692 Meysey Hampton, Glos. SU1199 Milton Keynes, Bucks. SP8440
Trifolium dubium	Ousel Valley, Bucks. SP8937 Little Wittenham, Oxon. SU5692 Meysey Hampton, Glos. SU1199 Milton Keynes, Bucks. SP8440

Table 6.1. The 10 study species and quadrat locations. The 4-figure grid reference is given.

This approach resulted in much less distortion than that using species abundances as raw data, since a space of only six dimensions was projected onto a two dimensional graph. The axes were also easier to interpret, because they could be related to plant traits or environmental properties directly. The end result is an ordination diagram which gives a visual indication of the extent to which the environment inhabited by each of the congeners is similar or dissimilar, and also if (and if so how) the environment of the paddocks differs from the range of environments occupied by the study species.

6.3 Results

Ordination diagrams for the five pairs of study species are shown at Figure 6.1 to Figure 6.5. For ease of interpretation, the variables with the heaviest loadings on the first two principal components are indicated on the diagrams. Further information about each ordination is given at Tables 6.2 - 6.6

6.3.1 *Cirsium vulgare* and *Cirsium eriophorum*

The ordination diagram for these species is shown at Figure 6.1. It shows a broad range of overlap between the two species, with perhaps a suggestion that *C. vulgare* is more prevalent in higher nutrient situations and extends into less basic sites than *C. eriophorum*. The grazing trial swards are more nutrient-rich than any of the *Cirsium* quadrats.

6.3.2 *Galium aparine* and *Galium verum*

The ordination diagram for these species is shown at Figure 6.2. It shows *G. aparine* occupying a rather narrow range on the first principal component, being characteristic of high competition and high nutrient situations whilst *G. verum* occupies a rather broader spread along the first principal component but is characteristic of more stressful, lower nutrient situations. There is little evidence of separation on the second principal component. In comparison with the vegetation around the target species, the vegetation of the paddocks is characterised by still higher competition and nutrient levels, together with a lesser ruderal element and more basic soils.

6.3.3 *Leontodon autumnalis* and *Leontodon hispidus*

The ordination diagram for these species is shown at Figure 6.3. There is a small degree of overlap between the two species, but *Leontodon autumnalis* is characteristic of more nutrient-rich and less stressful conditions compared with *L. hispidus*. The grazing trial swards appear, in comparison, more nutrient-rich and stressful than those in which *L. autumnalis* was observed and substantially more so than those occupied by *L. hispidus*. There is also a large difference in range occupied on the second axis, with the paddocks appearing to be more basic and moist than any sites from which either *Leontodon* species was recorded.

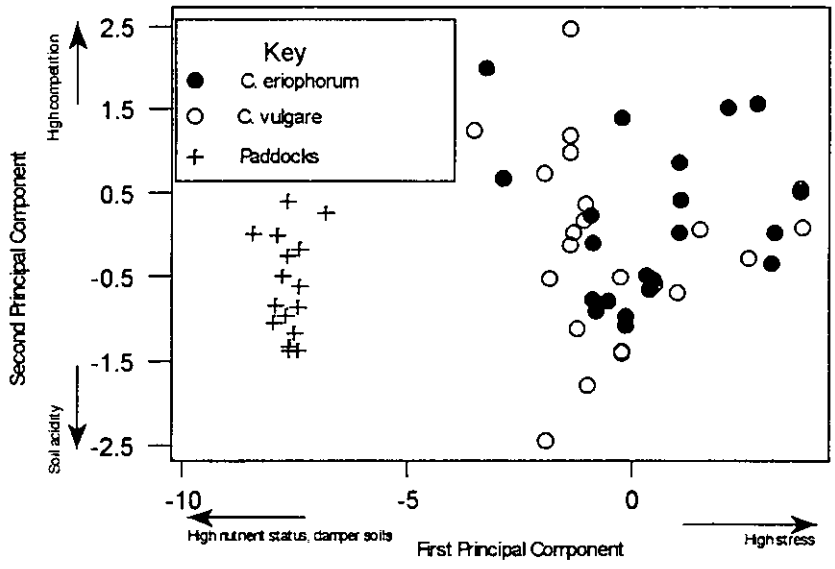


Figure 6.1. Ordination diagram for *Cirsium vulgare* and *C. eriophorum*.

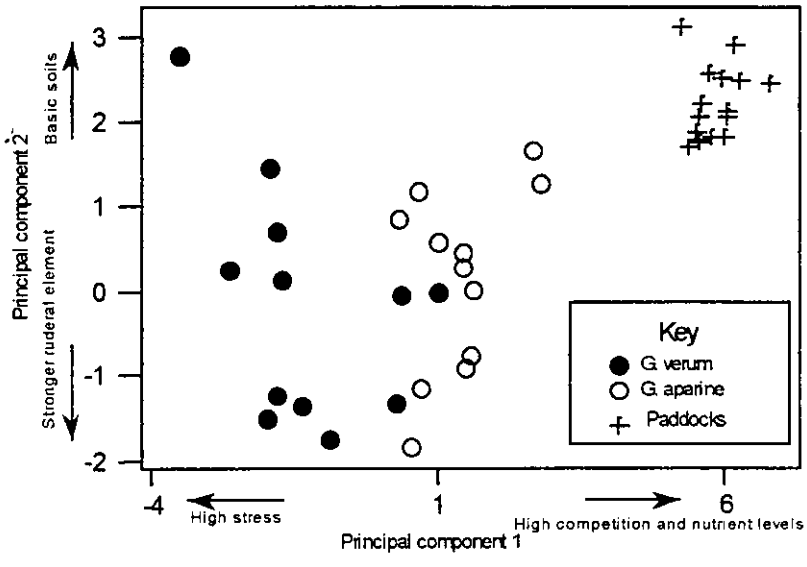


Figure 6.2. Ordination diagram for *Galium aparine* and *G. verum*.

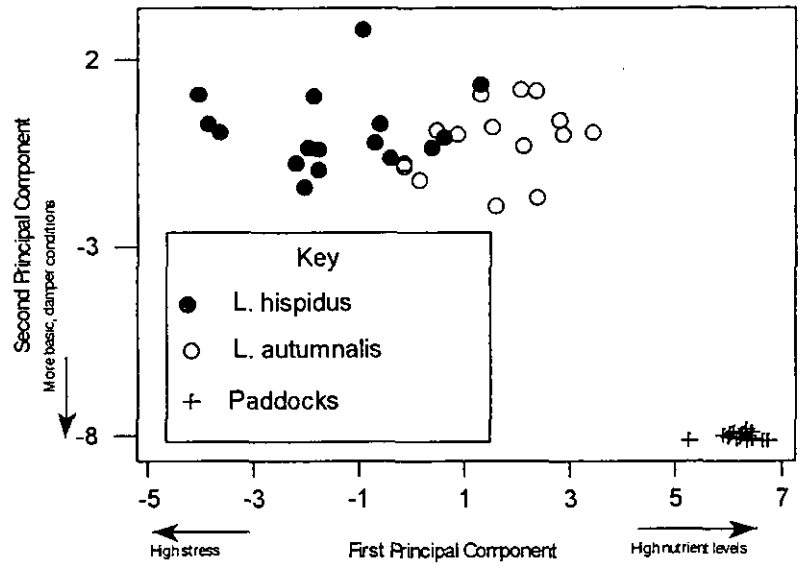


Figure 6.3. Ordination diagram for *Leontodon autumnalis* and *L. hispidus*.

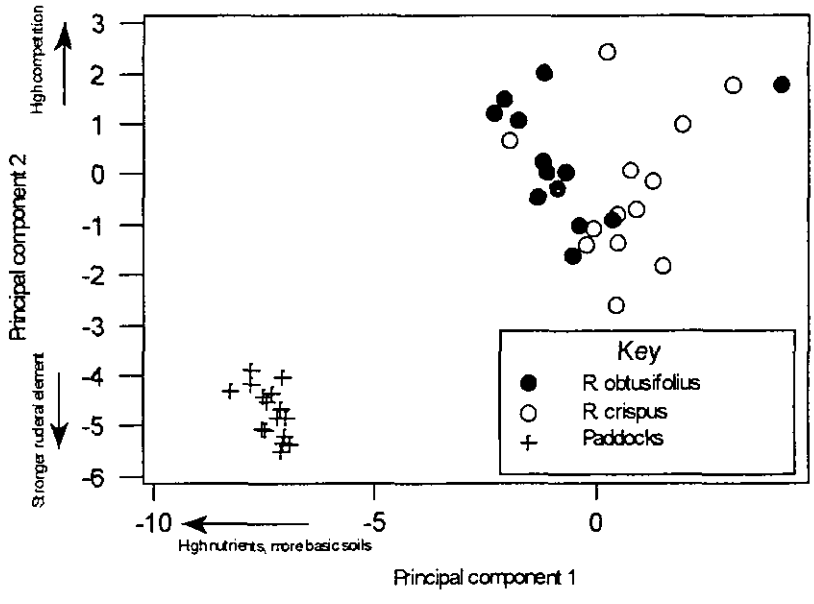


Figure 6.4. Ordination diagram for *Rumex crispus* and *R. obtusifolius*

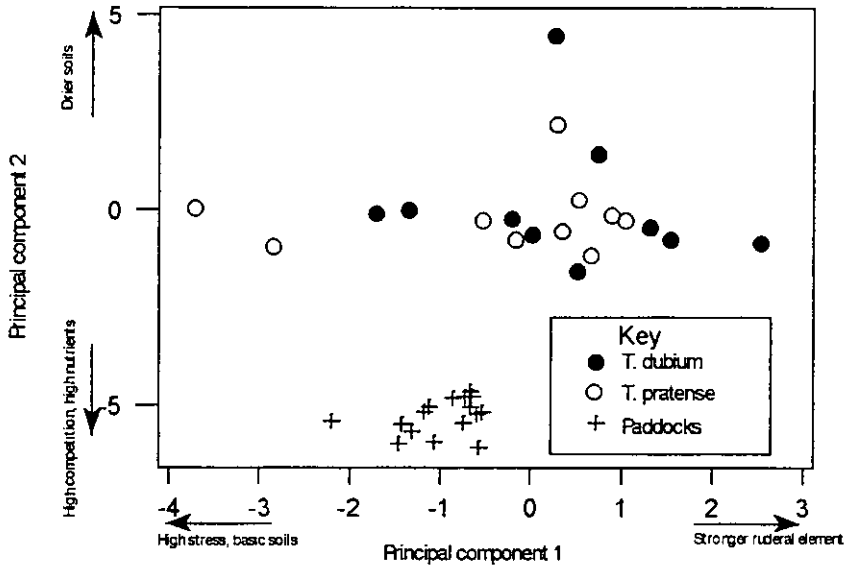


Figure 6.5. Ordination diagram for *Trifolium pratense* and *T. dubium*.

6.3.4 *Rumex crispus* and *Rumex obtusifolius*

The ordination diagram for these species is shown at Figure 6.4. There is a large amount of overlap between the two species, and no convincing evidence of ecological differences between the two species, except perhaps a suggestion that *R. crispus* may more frequently occur in lower nutrient less basic situations (higher scores on axis 1). Even here, however, the quadrat with the highest value on axis one was occupied by *R. obtusifolius*. The vegetation of the grazing trial appears characterised by lower competitiveness than the quadrats occupied by either *Rumex* species, and the soils of the paddocks also appear to be more basic and have a higher nutrient status than the *Rumex* quadrats

	First Component	Second Component
Eigenvalue	3.4779	1.0710
Proportion	0.580	0.178
Cumulative	0.580	0.758
Variable	**score on PC1**	**score on PC2**
C value	-0.420	0.414
S value	0.510	0.054
R value	-0.211	-0.862
Ellenberg F	-0.486	-0.078
Ellenberg R	-0.122	0.266
Ellenberg N	-0.518	0.079

Table 6.2. Principal components analysis for *Cirsium vulgare* and *C. eriophorum*.

	First Component	Second Component
Eigenvalue	3.0395	1.4927
Proportion	0.507	0.249
Cumulative	0.507	0.755
Variable	**score on PC1**	**score on PC2**
C value	0.536	0.039
S value	-0.516	0.249
R value	-0.083	-0.659
Ellenberg F	0.395	0.158
Ellenberg R	0.024	0.689
Ellenberg N	0.532	-0.049

Table 6.3. Principal components analysis for *Galium aparine* and *G. verum*.

	First Component	Second Component
Eigenvalue	4.2261	0.9994
Proportion	0.704	0.167
Cumulative	0.704	0.871
Variable	**score on PC1**	**score on PC2**
C value	0.409	0.043
S value	-0.475	-0.079
R value	0.452	-0.017
Ellenberg F	0.382	-0.405
Ellenberg R	-0.184	-0.901
Ellenberg N	0.473	-0.125

Table 6.4. Principal components analysis for *Leontodon autumnalis* and *L. hispidus*.

	First Component	Second Component
Eigenvalue	2.4666	1.7516
Proportion	0.411	0.292
Cumulative	0.411	0.703
Variable	**score on PC1**	**score on PC2**
C value	-0.323	0.622
S value	0.345	-0.019
R value	0.249	-0.609
Ellenberg F	-0.356	-0.333
Ellenberg R	-0.506	-0.343
Ellenberg N	-0.576	-0.117

Table 6.5. Principal components analysis for *Rumex crispus* and *R. obtusifolius*.

	First Component	Second Component
Eigenvalue	2.1622	1.8333
Proportion	0.360	0.306
Cumulative	0.360	0.666
Variable	**score on PC1**	**score on PC2**
C value	0.020	-0.616
S value	-0.633	0.160
R value	0.466	0.409
Ellenberg F	-0.204	-0.436
Ellenberg R	-0.468	-0.009
Ellenberg N	0.348	-0.488

Table 6.6. Principal components analysis for *Trifolium pratense* and *T. dubium*.

6.3.5 *Trifolium pratense* and *Trifolium dubium*

The ordination diagram for these species is shown at Figure 6.5. It shows a large amount of overlap between the two species, suggesting that there is little to distinguish them in terms of their ecological requirements. The vegetation of the grazing trial appears to be characterised by higher soil nutrient levels and higher levels of competition in comparison with the kind of vegetation often occupied by either of the *Trifolium* species.

6.4 Discussion

Perhaps the most striking general observation concerns the spatial relationship between the grazing trial quadrats and those of the pairs of congeners in Figures 6.1 to 6.5. In each of the figures, the paddocks are situated in a part of the ordination diagram associated either with higher levels of competition, higher nutrient levels or both, compared with the quadrats of the target species. The various field sites from which quadrat data were obtained were selected because they supported reasonably extensive populations of the target species and, to that extent, may be regarded as examples of 'good' habitat for the study species. The results of the ordination therefore suggest that the grazing trial is, to a greater or lesser extent, a sub-optimal habitat for these species which tend to flourish best in less competitive or lower nutrient situations. In a study of the grazing trial, Watt *et al.* (1996) note that the residual fertility of the site "makes succession towards a more diverse flora a slow process".

Quadrat data for congeneric pairs were 'matched' within sites wherever possible. In other words, when one member of a pair was recorded from a site, every effort was made to find and record quadrat data for the other. An alternative approach would be to identify a wide

range of sites for each species in different locations and subject to different environmental conditions. In this way it would be possible to build up a fuller picture of the niche occupancy for each species, but it would entail a vastly greater amount of time than was available to me. I therefore adopted the pair-wise approach described here in order to avoid confounding potential niche differences between species with site differences. This approach is, however, likely to show smaller niche differences than would be found in a fuller study, and should be borne in mind when interpreting the results. Given this caveat, what conclusions can be drawn about the individual pairs of species investigated here?

On the *Cirsium* ordination diagram, the plants occupying the most extreme positions on the two axes are all individuals of *C. vulgare*, although the difference between individuals of *C. vulgare* and *C. eriophorum* is very slight along the first axis. *C. vulgare* does grow very successfully under at least some of the treatments of the grazing trial, although population sizes vary from year to year. More work along the lines of that undertaken here would undoubtedly expand its niche range on the diagram. Field experience suggests, however, that the niche range of *C. eriophorum* would not be enlarged to the same extent (see Appendix 1). In several localities visited during the work for this chapter (Crickley Hill, Glos; Sharnbrook, Beds; Aston Upthorpe, Berks and Cherhill Down, Wilts), *C. vulgare* and *C. eriophorum* were studied growing together in coarse grassland, and *C. vulgare* was seen to extend into adjacent intensively managed and heavily grazed grassland in contrast to *C. eriophorum* which was absent. Overall, the ordination and field observations suggest not so much niche differentiation in the two *Cirsium* species as a broader niche occupancy for *C. vulgare*. On this basis, *C. vulgare* appears to be somewhat better suited than *C. eriophorum* to the environment of the paddocks. In the seedling experiment reported in Chapter 4, *C. eriophorum* generally outperformed *C. vulgare*, although the reverse was the case when a later stage of growth was investigated in Chapter 5. The experiment reported

in the Chapter 7 suggests that *C. eriophorum* suffers a greater proportion of biomass loss through defoliation than *C. vulgare* and has a lower growth rate. This may in part be the reason for the absence of *C. eriophorum* from the grazing trial. It is difficult to compare the overall suitability of the two *Cirsium* species for conditions in the grazing trial from the field experiments alone because they were not run for the complete life cycle of the plants. In these circumstances the ordination and field observations perhaps give the best guidance, and suggest that *C. vulgare* is better suited to conditions in the paddocks.

For the two *Galium* species, the ordination diagram suggests a certain amount of niche separation. If a measure of vegetation structure (e.g. mean vegetation height) had been recorded for the quadrats, the amount of niche separation would almost certainly appear greater. During the course of the fieldwork, *G. aparine* could always be found at the same sites as *G. verum*, but almost invariably sprawling over patches of taller vegetation. *G. aparine* appears from the ordination to occupy situations which are most similar to those prevailing at the grazing trial, occurring towards the more competitive and nutrient-rich part of the diagram. In terms of vegetation height however, the conditions in the grazing trial are generally more similar to those in which *G. verum* was found rather then *G. aparine* (R.Tofts, pers. obs.), a fact which may render the grazing trial less suitable for *G. aparine* than might appear from the ordination diagram alone. The results of the seedling experiment indicate that either *Galium* species may outperform the other, depending upon the combination of experimental conditions being considered. The experiment reported in Chapter 5 suggests that *G. verum* is able to survive and grow in the grazing trial, particularly in winter-grazed plots, although the experiment was not continued for long enough to fully compare the performance of the two *Galium* species. Overall, the field

observations and experimental work suggest that *G. verum* is reasonably well suited to conditions in the grazing trial and its absence appears to result from dispersal limitation.

Based on the evidence of the ordination diagram, there appears to be niche separation between the two *Leontodon* species, and *L. autumnalis* seems to be the better suited of the two to conditions at the grazing trial. Of all five pairs of congeners studied here, it proved most difficult to find populations of both *Leontododon* species at the same sites, a fact consistent with important ecological differences. Even so, the conditions at the grazing trial appear to be far from ideal for *L. autumnalis*, and it is perhaps noteworthy that this species is uncommon within the grazing trial. The poor seed viability of *L. autumnalis* makes it impossible to compare its performance with *L. hispidus* in the early stages of growth. No significant differences in performance were recorded between the two *Leontodon* species in the experiment reported in Chapter 5, although *L. autumnalis* did show a slightly higher survival probability than *L. hispidus*. Possibly this result would have been more marked if the experiment had been run for a longer period of time. If the poor viability of the *L. autumnalis* seed is ignored on the grounds that it is probably atypical, there is some evidence from the experiments and ordination that *L. autumnalis* is slightly better suited to conditions in the grazing trial.

The ordination diagram shows substantial niche overlap between the *Rumex* congeners. Neither appears substantially better suited to conditions in the grazing trial. In one of the quadrat sites (Chulmleigh, Devon) both *Rumex* species were observed growing in *Lolium*-dominated pasture similar to that of the grazing trial, but in the other sites they occurred in rough grassland with competitive species such as *Elytrigia repens*. In the seedling experiment, *R. obtusifolius* initially outperformed *R. crispus*, but this difference in performance had disappeared by the two true-leaf stage, and the situation was reversed

during the later stage of growth examined in Chapter 5. Taking into account both experimental and ordination studies, *R. crispus* is perhaps marginally better suited to conditions in the grazing trial, but the difference in performance appears only slight.

There appears to be no reason to suppose that either of the *Trifolium* species is better suited to growing in the paddocks than the other on the basis of the ordination diagram, which shows substantial niche overlap despite the life history differences between the two species. It is, however, possible that niche differences exist but at a scale too small to be detected by a 1 m^2 quadrat. *T. dubium* performed much better than *T. pratense* in the seedling experiment due to heavy seed predation on the latter species. The reverse was the case, however, during the later growth stage examined in Chapter 5. A full comparison between the two species based on the experimental results is not possible, since one species (*T. dubium*) is an annual and the other a perennial and the second experiment was run for long enough for *T. dubium* to complete its life cycle but not *T. pratense*. Nevertheless, the evidence from both experiments and the ordination does at least suggest that *T. dubium* seems well enough suited to conditions in the grazing trial to survive and persist there once initial establishment is achieved.

Chapter 7. Plant traits in relation to their performance in different environments: a study using *Cirsium eriophorum* and *Cirsium vulgare*

7.1 Introduction

In this chapter I report the results of two comparative greenhouse experiments on *Cirsium eriophorum* and *C. vulgare*, examining plant performance in relation to nutrient level and defoliation. The choice of these two species was made in order to obtain information for use in a forthcoming Biological Flora (see Appendix 1). The results from these experiments are, however, relevant to the wider questions asked in this thesis. In Chapter 3, for example, I suggested that part of the difficulty in predicting species presence/absence or species abundance in a community lay in the absence of information on some potentially important traits. In the context of the Little Wittenham experiment (a grazed community on relatively nutrient rich soils), it is relevant to ask whether data on the response of plants to defoliation and nutrient levels are helpful in interpreting the plants' distribution and abundance in nature. Constraints of time limited this study to only one pair of congeners, but there is a considerable amount of information on the distribution and performance of these two species in nature elsewhere in this thesis and (for *C. vulgare*) in the literature. It may therefore be possible to draw qualitative if not quantitative conclusions about the potential use of additional traits in predicting community assembly.

At the national scale, the distribution of *C. vulgare* (ubiquitous except in mountainous parts) is much wider than *C. eriophorum* (restricted to calcareous substrates and seldom occurring further north than the Peak District - see Appendix 1). At the smaller scale, *C. vulgare* again seems to be more widely distributed, being often abundant in grasslands managed for modern commercial grazing as well as occurring under more traditional management regimes. These differences suggest that *C. vulgare* may have a greater ecological amplitude than *C. eriophorum*. Can this apparently greater amplitude be linked to biological characteristics of the plants? Field observations suggested four hypotheses which might account for this apparent difference in distribution:

i) *C. eriophorum* has a lower growth rate soon after germination in comparison with *C. vulgare* and is therefore more likely to be ousted by competing species.

ii) *C. eriophorum* is less able than *C. vulgare* to tolerate the intense grazing to which agricultural grasslands are subject.

iii) *C. eriophorum* is less able than *C. vulgare* to tolerate or utilise the relatively high levels of nutrients prevalent in many agricultural grasslands, and

iv) the early leaves of *C. eriophorum* are more erect in habit than those of *C. vulgare*, and grazing to a particular sward height results in correspondingly greater loss of biomass for *C. eriophorum*.

Hypothesis *iv)* is therefore a special case of hypothesis *ii)*. In experiment 1 the first three hypotheses are examined. Experiment 2 is designed to examine hypothesis iv), but also allows hypotheses *i)* and *ii)* to be investigated.

7.2 Methods

7.2.1 Experiment 1

180 seeds each of *C. eriophorum* and *C. vulgare* were sown into Plantpak P180 plug trays filled with John Innes seed compost on 4 April 1997 and watered as required. The experiment was run in an unheated greenhouse at the Open University. On 20 April, 40 plugs of each species at the same stage of development (2 true leaves) were removed and re-potted into 9 cm pots filled with John Innes No.2 compost and arranged into 5 blocks of 16 pots (8 pots of each species in a randomised arrangement) and watered. On 23 April, the following experimental treatments were imposed: *i)* simulated grazing - plants were either cut back to the cotyledons (simulated grazing) or allowed to grow unhindered, and *ii)* nutrient level - plants were either watered as required with 25 ml tap water or 25 ml NPK fertiliser solution (at 1.5 g fertiliser per litre of water). This level of fertiliser application was chosen on the basis of information provided by Phostrogen Ltd., in order to provide a slight excess of nutrients. This is not designed to mimic the situation in the field, but simply to provide two contrasting nutrient levels over which the species may be compared. The treatments were applied in a fully factorial manner in a randomised blocks design. This resulted in a 2x2x2 (species x grazing x fertiliser) factorial design with 2 replicates in each of 5 blocks. On average, plants were watered or fertilised approximately 3 times per week. This was continued until 19 May at which time the plants were harvested, had the soil washed from their roots and were then oven dried for 48 hours at 80^{0}C (further drying resulted in no further detectable weight loss). Total dry weight (square root transformed) was used as the dependent variable in a factorial analysis of variance. Hypothesis *i)* (that *C. eriophorum* has a lower growth rate soon after

germination in comparison with *C. vulgare*) suggests that a main species effect will be observed, with *C. vulgare* having the higher biomass. Hypothesis *ii)* (that *C. eriophorum* is less able than *C. vulgare* to tolerate defoliation) suggests that a species x cutting interaction will be observed, with *C. eriophorum* biomass being disproportionately reduced by cutting. Hypothesis *iii)* (that *C. eriophorum* is less able to tolerate or utilise high nutrient levels) suggests that a species x fertiliser interaction will be observed, with *C. eriophorum* accumulating relatively less extra biomass when fertilised that *C. vulgare*.

7.2.2 Experiment 2

On 2 June 1997, seeds of *C. vulgare* and *C. eriophorum* were sown as described in experiment 1, and 18 plants of each species at the same stage of development (three true leaves showing) were planted into 9 cm pots on 11 July 1997. The pots were completely filled with John Innes No.2 compost, thus leaving no projecting pot rim, and were watered as required. The experimental arrangement used three pots of each species randomly arranged in each of six blocks. On 18th July the following treatments were imposed randomly on each of the two species in each block *i)* uncut, *ii)* leaves cut to a height of 2 cm above the soil surface, and *iii)* leaves cut to a height of 4 cm above the soil surface. Cutting was undertaken at approximately 10 day intervals (resulting in five harvests), and was continued until 28th August. All cut material was dried and weighed as described in section 7.2.1, and on 28th August all plants were removed from their pots, root washed and dried.

The proportional difference in biomass (between a given treatment and another treatment which may be regarded as a control) may be as informative as an absolute difference when one is considering the impact of a particular treatment on a plant, since a loss of 75%

biomass in a small plant, for example, is likely to be much more 'costly' than a 10% biomass loss in a larger plant despite possibly constituting a smaller absolute loss. Beyond examining the cumulative loss of biomass for the two species, three analyses were therefore performed: *i)* ANOVA on the final biomass values of the plants, *ii)* ANOVA on the proportion of final total biomass (in relation to the uncut control) for the two (2 cm and 4 cm) cutting heights, and *iii)* ANOVA on the amount of biomass removed during the course of cutting.

7.3 Results

7.3.1 Experiment 1

The analysis of final biomass is given at Table 7.1. It was necessary to square root transform the dependent variable in order to meet the assumptions of the analysis. Statistically significant effects were identified for species and cutting and the interaction between species and cutting, and also fertility. The results (back transformed) for species and cutting are shown at Figure 7.1. When cut, final biomass of *C. eriophorum* was 0.49g compared with *C. vulgare* at 0.75g. When uncut, the corresponding values were 1.95g and 3.02g respectively. Fertiliser addition resulted in a significant (p=0.001) increase in biomass (1.67g *vs.* 1.08g, averaged across treatments and back transformed).

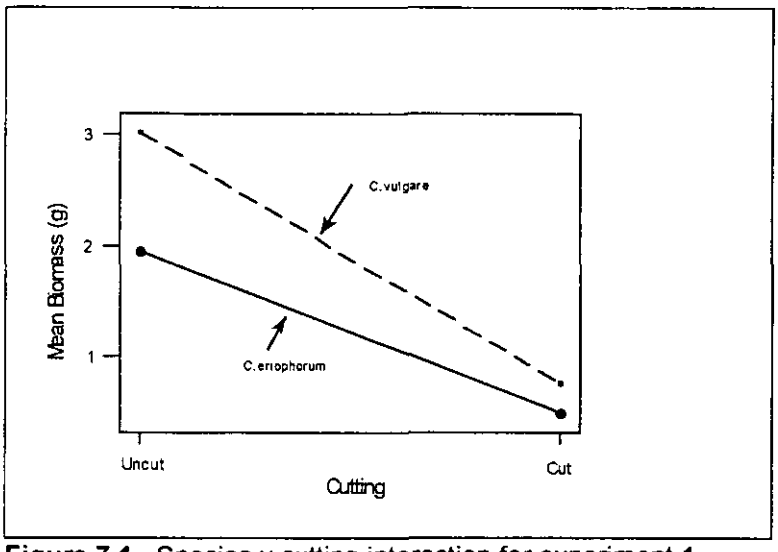


Figure 7.1. Species x cutting interaction for experiment 1.

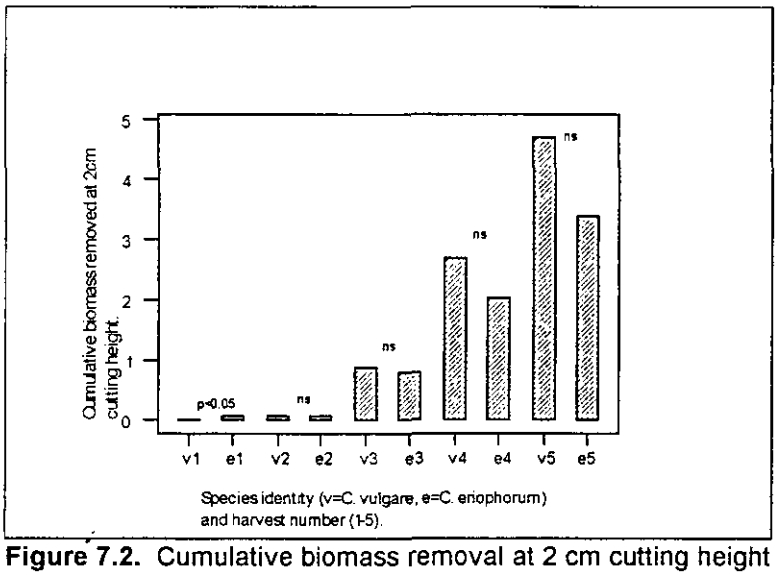


Figure 7.2. Cumulative biomass removal at 2 cm cutting height for experiment 2.

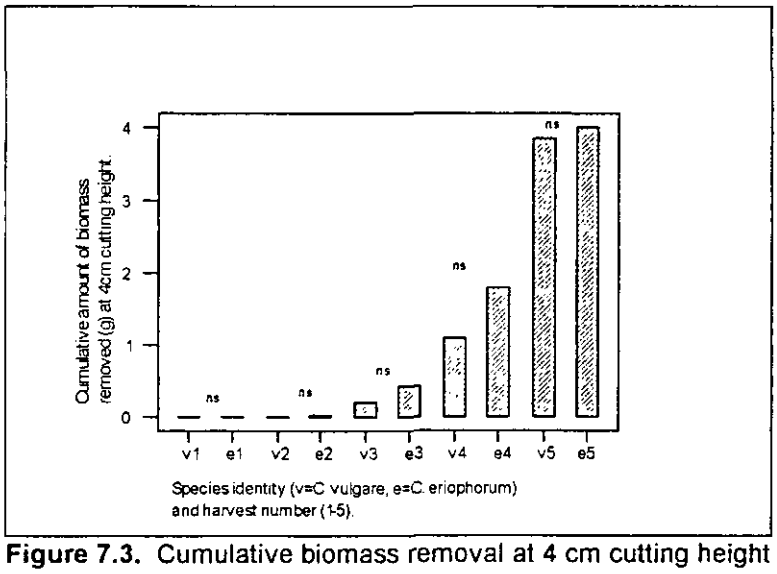


Figure 7.3. Cumulative biomass removal at 4 cm cutting height for experiment 2.

Treatment	df	ss	ms	F	Significance
Species (S)	1	1.2927	1.2927	78.24	**p=0.000**
Cutting (C)	1	12.3702	12.3702	748.74	**p=0.000**
Fertility (F)	1	0.2062	0.2062	12.48	**p=0.001**
Block (B)	4	0.1167	0.0292	1.77	p=0.146
S x C	1	0.1430	0.1430	8.65	**p=0.004**
S x F	1	0.0003	0.0003	0.02	p=0.901
C x F	1	0.0263	0.0263	1.59	p=0.211
S x C x F	1	0.0163	0.0163	0.99	p=0.324
Error	68	1.1235	0.0165		
Total	79	15.2951			

Table 7.1. ANOVA for final biomass, Experiment 1. The dependent variable is square root transformed total plant biomass. Bonferroni corrected 5% cut-off point at p=0.0064.

7.3.2 Experiment 2

The cumulative amount of biomass removed for both thistle species under the two cutting regimes is shown at Figures 7.2 and 7.3. When a simulated sward height of 2 cm was maintained, *Cirsium eriophorum* initially lost significantly more biomass than *C. vulgare*. By the end of the experiment, however, *C. vulgare* had lost a greater amount of biomass although this difference was not statistically significant. When a simulated sward height of 4 cm was maintained, *C. eriophorum* continued to suffer the highest losses of biomass throughout the course of the experiment (except at the first harvest when no plants of either species had any leaves extending to 4 cm above soil level), although in no case was this difference statistically significant.

Table 7.2 shows the effects of species and cutting height on final biomass. The dependent variable was square root transformed to meet the assumptions of the analysis. The results with regard to species identity indicate that *C. vulgare* had a significantly (p<0.001) greater final biomass than *C. eriophorum* (5.94 g *vs.* 2.24 g, averaged over all cutting treatments and back transformed). Cutting height also had the expected effect, with final biomass

being greatest in uncut plants, intermediate in those cut to 4 cm and least in those cut to 2 cm (means averaged over species and back transformed: 5.99 g, 3.94 g and 2.27 g respectively). There was no evidence of an interaction between species and cutting height.

Treatment	df	ss	ms	F	Significance
Species (S)	1	7.9787	7.9787	52.35	p=0.000
Cutting height (H)	2	4.8468	2.4234	15.90	p=0.000
Block	5	0.9077	0.1815	1.19	p=0.342
S x H	2	0.6944	0.3472	2.28	p=0.123
Error	25	3.8102	0.1524		
Total	35	18.2378			

Table 7.2. ANOVA for final biomass (square root transformed). Bonferroni corrected 5% cut-off point at p=0.0127.

An analysis of ~~the proportion of~~ final biomass (expressed as a proportion of the biomass of the uncut control, and log transformed) is given at Table 7.3. In this case an analysis of proportions is being undertaken, but the dependent variable does not simply take values between 0 and 1 (or 0% and 100%). It can exceed unity in cases where the biomass value exceeds that of the control against which it is being compared. This restricts the methods of analysis which may be used. In the event, the proportional data were examined for violation of the standard assumptions of ANOVA, and it was found that a logarithmic transformation would enable an ANOVA to be undertaken. The ~~proportion of loss of~~ final biomass as a proportion control biomass was significantly lower (p=0.001) in the case of *C. eriophorum* (30.5% of the control value for *C. eriophorum vs.* 69.9% for *C. vulgare*, back transformed). The effect of cutting height was also statistically significant, with 2 cm cutting reducing the proportion compared with 4 cm cutting as expected (34.8% vs. 61.3% respectively, back transformed).

Treatment	df	ss	ms	F	Significance
Species (S)	1	4.1357	4.1357	18.77	p=**0.001**
Cutting height (H)	1	1.9132	1.9132	8.68	p=0.010
Block	5	2.4693	0.4939	2.24	p=0.104
S x H	1	0.0158	0.0158	0.07	p=0.792
Error	15	3.3056	0.2204		
Total	23	11.8396			

Table 7.3. ANOVA for proportion of final biomass (in relation to uncut control, and log transformed). Bonferroni corrected 5% cut-off point at p=0.0127.

The ANOVA for total biomass removed is given at Table 7.4. There was no significant difference between the two species in amount of biomass removed. More surprisingly, no significant difference was detected between the two cutting heights by the end of the experiment. Figures 7.1 and 7.2 indicate that more biomass was lost at an earlier stage with the 2 cm cutting treatment, but by the end of the experiment, the marginally greater loss under the 2 cm cutting regime was largely obscured by other (random) effects.

Treatment	df	ss	ms	F	Significance
Species (S)	1	0.0379	0.0379	0.18	p=0.678
Cutting height (H)	1	0.4315	0.4315	2.03	p=0.174
Block	5	1.2641	0.2528	1.19	p=0.359
S x H	1	0.4061	0.4061	1.91	p=0.187
Error	15	3.1827	0.2122		
Total	23	5.3223			

Table 7.4. ANOVA for biomass removed during the course of experiment 2. Bonferroni corrected 5% cut-off point at p=0.0127.

7.4 Discussion

In section 7.1, four hypotheses were offered which may (at least partly) account for the small-scale distributional differences between *Cirsium eriophorum* and *C. vulgare*. The findings reported in this chapter support three of these hypotheses (at least in part) but not the other. They also invite comparison with the field data reported elsewhere in this thesis. Hypothesis *i)* (that *C. eriophorum* has a lower growth rate than *C. vulgare* shortly after

germination) was strongly supported by both experiments. There is evidence (Grime *et al.* 1997b) of a 'decoupling' between attributes relating to the regenerative and mature phases of plant growth, and there are many instances of regenerative attributes playing a key role in the organisation of plant communities (e.g. see review by Grubb 1977, also Thompson *et al.*, 1996). It therefore seems reasonable to suppose that the characteristics of plants soon after germination revealed over a short term experiment may have a bearing on their presence or absence over the long term in plant communities. In the present case, the result was in accordance with the initial hypothesis. There is strong evidence to suggest that *C. vulgare* accumulates biomass more rapidly than *C. eriophorum* in the early stages after germination, and does so under a range of different conditions (different degrees of defoliation and different nutrient regimes). This characteristic seems likely to confer benefits in grasslands subject to modern agricultural practices.

Hypothesis *ii)* (that *C. eriophorum* was less able to withstand defoliation compared with *C. vulgare*) was not supported when absolute biomass loss was considered (experiment 1), but was supported when proportionate loss (in comparison with uncut controls) was considered (experiment 2). When total final biomass was analysed in experiment 1 (i.e. an *absolute* measurement), a species x cutting interaction was identified which indicated that *C. eriophorum* was in fact less affected by cutting than *C. vulgare* although this statistically significant result (p=0.004) was small in magnitude (see Figure 7.1), and a comparable result was not identified in experiment 2. When analysed in terms of the proportion of biomass lost in relation to an uncut control rather than as an absolute measurement, significant differences between the species were observed. When cut to a particular height (2 cm or 4 cm), the biomass in comparison with the control value was significantly lower for *C. eriophorum* compared with *C. vulgare* during the course of the experiment (30.5% *vs*, 69.9% respectively).

Hypothesis *iii)* (that *C. eriophorum* was less able to tolerate or utilise high levels of nutrients compared with *C. vulgare*) was not supported. Nutrient addition (experiment 1) led to a significant (p=0.001) biomass increase in both species, but there was no evidence of any interaction between species and nutrient level (p=0.901). The fact that the species were only examined in isolation rather than in an environment where competition may complicate the relationship between nutrient levels and plant performance must, however, be borne in mind (cf. McGraw and Chapin 1989).

Hypothesis *iv)* (that *C. eriophorum* suffers a greater loss of biomass when cut back to a certain height compared with *C. vulgare*) was supported to some extent, although the relationship between cutting height and biomass lost varied through time, depended on the height at which defoliation took place, and also on the precise way in which the question was examined. When cut to 2 cm above soil level, *C. eriophorum* initially lost significantly more biomass in absolute terms than *C. vulgare* (Figure 7.2, harvest 1), due to its more erect early leaves. The more rapid growth of *C. vulgare*, however, caused the cumulative loss of biomass of that species to be greater than the amount lost by *C. eriophorum* by the end of the experiment, although this difference was not statistically significant. When cut to 4 cm above soil level, *C. eriophorum* lost more biomass in all cases (except harvest 1 when neither species had any leaves extending to 4 cm in height), again a result of its more erect leaves, although this difference was never statistically significant. When analysed as a proportional loss of biomass compared with an uncut control, *C. eriophorum* was found to lose a significantly greater amount of biomass (as discussed under hypothesis *ii*.).

How do these results fit in with the other observations and experiments reported in this thesis? The ordination diagram for *Cirsium* in Chapter 6 (Figure 6.1) shows a broad range

of niche overlap, but also suggests that *C. vulgare* has a broader range of niche occupancy than *C. eriophorum*. As argued in Chapter 6, the results of the ordination are likely to show less extreme separation than may be found if the total ranges of the species are considered. Field observations (see section 6.4 and also Appendix 1) suggest that *C. vulgare* is better able to tolerate conditions of heavy grazing than *C. eriophorum*, and the experimental results obtained here are consistent with what was observed in the field. The results of the experiment in Chapter 4 suggest that *C. eriophorum* generally outperforms *C. vulgare* in the grazing trial, during the earlier stages of growth, but the results of the experiment in Chapter 5 relate to growth after the two true-leaf stage, and are more easily comparable with the findings reported here. The latter results are consistent with the findings reported here, indicating that plugs of *C. vulgare* performing significantly better than those of *C. eriophorum* under grazing.

What are the wider implications of this work for trait-based studies? In Chapter 3, it proved possible to link species presence in or absence from a community to several traits. It is not surprising that the traits examined in that chapter did not exhaust the list of 'useful' ones. There are many other properties of plants which may be informative when one wishes to investigate how they will perform in a particular environment (e.g. Grime *et al.* 1997b, Boutin and Keddy 1993). In this chapter I investigate yet further traits. This begs the following question: 'how many traits need to be quantified before one can understand why plants grow where they do?' I can offer no answer to this important question, although it is worth observing that even with regard to the tightly circumscribed question examined here, there are additional traits such as palatability and visibility to grazers which must be considered in order to understand the relationship between community composition and defoliation.

What the results of this study do suggest is that whilst it is possible to link aspects of a species' biology to its distribution in communities, the choice of what traits to measure should be based on a good knowledge of the species in the field. Some differences between closely related species may be important predictors of presence or absence from a community but be far from obvious (e.g. a difference in leaf attitude during the early stages of growth) if one is just conducting a desk-based study. In addition, traits which are important in separating some species on the basis of their ecological requirements may not be useful in separating others. This possibility is very relevant to the formulation of assembly rules, and is discussed in the concluding chapter.

Chapter 8. Discussion

8.1 Competition or the environment: what structures community composition?

In Chapter 1 I discussed two opposing theories about which processes control the assembly of ecological communities. If controlled primarily by competition, the species forming communities are (according to classical theory) anticipated to be less similar than expected by chance. If, on the other hand, the environment plays the key role in community organisation, the expectation is that species will be more similar than dictated by chance. Resolving this apparent paradox is, however, not just an exercise in ecological theory. The processes which govern community assembly also govern how, and to what extent, we can model community assembly. If classical competition theory is correct, we will anticipate a tendency for species to be dissimilar, but this then begs the question 'dissimilar to what?' On the basis of competition theory, it will be impossible to predict whether a given species (or type of species) is likely to enter a community or not unless we already have information about the species (or types of species) that are there already. This severely constrains the degree to which predictions can be made. Thus theory suggests that only very weak predictions would be possible in the early successional communities, a hypothesis that was tested (and found wanting) on plant communities by O'Connor and Aarssen (1987). The quality of predictions about later successional communities will depend upon the extent of knowledge about their current species composition. A view of small mammal community assembly along competitive lines is offered by Brown and co-workers (e.g. Fox and Brown 1993 and examined critically by Stone *et al.* 1996) in which species are organised into functional groups. The authors state that "there is a higher probability that each species entering a community [from a pool of species] will be drawn from a different functional group until each group [in the pool] is represented, and then the rule repeats". If this is the

case, knowledge about present community composition is essential before future predictions may be made. If the environment plays the major role in community assembly, however, the situation is different. If we can specify the environment and know the relationship between species characteristics (e.g. traits) and environmental conditions we will be able to offer predictions about what species are likely to grow in a locality on an individual basis, without needing to know about the presence (or abundance) of other species in the community.

Do the findings reported in this thesis favour one of these hypotheses over the other? In Chapter 3, I adopted a large-scale (whole community) approach based upon species traits in an attempt to link the presence and ranked abundance of species in the grazing trial to selected biological characteristics. Several significant relationships between traits and presence in the grazing trial were found, and in all statistically significant cases, trait under-dispersion associated with differences in trait value was recorded. These facts support the idea that the environment structures community assembly. Rather than reflecting a lack of importance on the part of competition in structuring the plant community, however, in my view the lack of convincing trait overdispersion reflects the scale at which the study was undertaken (but see comments below). In a study of small scale community composition (e.g. a series of 10 cm^2 quadrats), the number of species within each quadrat will be small, and each species may be able (in theory at least) to interfere with the others. Coexistence between species at this scale may well tend to occur preferentially between members of different guilds, due to competitive exclusion, as has been suggested elsewhere (e.g. Wilson and Watkins 1994, Wilson *et al.* 1995b). There is weak evidence of limitations to species coexistence at the micro-scale (2 mm diameter circular quadrats) at the Little Wittenham grazing trial (Wilson *et al.* 1996c). In the case of plant communities, therefore, the relative immobility of species suggests that the effects of competition on community structure may be most evident at the scale over which plants influence one another. In the area occupied by a community, there is likely to be plenty of space in which species which would not tolerate one another as neighbours can occur at a comfortable distance from one another.

Microhabitat heterogeneity also allows for different kinds of species to exist in close proximity in the community.

There is, however, also potential for competition to leave its mark on community composition at a larger scale, as suggested by the findings of Chapter 3 where competitive ability was found to be significantly higher in plants which grew within the grazing trial compared with other species in the species pool. It seems quite possible that, in a nutrient-rich site, the environment favours those species with a high competitive ability and to that extent, both environmental and competitive explanations may partially account for species presence or abundance at a particular scale. In plant communities studied at a large scale, however, it is harder to identify competition unequivocally as a force which shapes community assembly because one has to compare plants on the basis of some general measure of competitiveness (e.g. the C value used in Chapter 3). At a small scale, stronger patterns may be seen and firmer conclusions drawn, because neighbouring species may be examined and evidence for niche separation sought. In studies of fauna, competition is usually envisaged as a force structuring community composition over a wider area (e.g. up to about 5 ha, Bowers and Brown 1982) than is usually considered for plants, due to the way animals can range (and interfere with one another) over large areas. It is perhaps worth adding that occasionally, large scale effects of interspecific competition have been claimed for plants. Following an observation by Darwin, Rejmánek (1996) has suggested that the species composition on the scale of a continent bears the imprint of interspecific competition.

8.2 Trait data

The benefits of basing assembly models on species attributes or an ecological classification scheme (rather than just species identities) are clear, and various ways of doing this have been mentioned (section 1.5). I make no attempt here to discuss the merits of the different methods, but concentrate on some key issues relating to the use of traits. The traits quantified in Chapter 3 were, of necessity, restricted to published sources. In some cases (e.g. longevity) these were rather crudely categorised or quantified and even if such traits are of great importance in influencing community assembly, models using crudely quantified traits can be expected to offer no more than crude predictions. Screening species for trait data is, however, a vast undertaking, and even the acquisition of data about response to nutrient input and biomass removal under different fertiliser and defoliation regimes for two species (Chapter 7) involved a substantial amount of work. For the foreseeable future, ecological predictions will probably have to be made with trait data at a similar level of detail to those we now possess.

The relationship between the characteristics and performance of plants was much clearer when the traits were used to predict establishment from the species pool (Chapter 3) than when an attempt was made to understand the results of small scale (within community) experiments in terms of biological characteristics. In the case of establishment from the species pool, in every case which showed statistical significance, a result was seen in the expected direction. This was not the case in the experiments where, in several cases, the experimental findings either ran contrary to initial expectation or (in the case of some interactions with grazing regime) could not be given a ready biological interpretation even in retrospect. Complex grazing effects have also been found by Silvertown *et al.* (1992).

This suggests that, at the level of detail currently available, trait data are probably most useful in large scale studies where one is interested in identifying those species from the species pool most likely to be present (or those species likely to be most abundant) in a community. It seems clear from the number of strongly significant effects detected in the field experiments, that the unexpected or unpredicted results do not just record chance differences in performance between ecologically equivalent species. If this is so, then the results must be linked to *some* biological process or other. The greenhouse investigation into the two *Cirsium* species reported in Chapter 7 suggests that detailed comparison of similar species may reveal important (and easily overlooked) characteristics in which they differ and that such differences may be linked to differences in performance in various environments. Differences in leaf demography have also been identified (Sydes 1984) which are potentially important in influencing species performance. It is, however, impracticable to undertake such experiments for all the species which might inhabit a community. In Chapter 6, some species which clearly differed on the basis of an apparently important biological characteristic (e.g. the annual *Trifolium dubium* and perennial *T. pratense*) did not show any clear differences in the communities they inhabited. Other species (e.g. *Leontodon hispidus* and *L. autumnalis*) which might appear to be more biologically similar showed much clearer differentiation in the communities where they grew. This again supports the view that, at the small scale, it may be difficult to predict species performance on the basis of easily recorded traits.

Leaving aside the difficulties of quantifying traits in a sensitive way, problems may arise because of the way in which individuals of the same species may differ from one another. There may, for example, be a genetic basis for differences in trait value (e.g. Houssard and Escarré 1995, Berkefeld 1988), creating the problem of what value to assign to a species. Such difficulties would remain, however, even if species identity rather than trait value were

used in an assembly model. Differences in trait value within species will add a further component of noise to a system which is influenced by many factors which may be hard or impossible to predict.

8.3 Predictability and randomness

Attempting to discover why an extant community contains a particular set of species is of fundamental importance in developing models of community assembly. If it proves impossible to account for current species composition, any attempt to predict community changes resulting from changing environmental conditions will be futile. The results reported in this thesis do not enable a quantification of the degree of randomness or unpredictability in community assembly. They do, however, suggest that whilst community assembly may be to some extent predicted on the basis of plant traits, a substantial amount of variability remains unaccounted for.

The experiments described in Chapters 4 and 5 suggest that dispersal limitation may have a strong effect on community composition. This is in agreement with work reported elsewhere (e.g. Primack and Miao 1992, Tilman 1997). Dispersal limitation is perhaps the most unpredictable link in the community assembly chain. The availability of seeds or other propagules (which depends in turn upon imponderables such as weather conditions and may vary greatly from year to year) must coincide with the availability of vacant microsites in the community and also with the agents of dispersal. Thus for wind dispersed seeds, the wind must be sufficiently strong and in the right direction at the time of seed release for the seeds to travel from the parent plant to vacant microsites. Propagule dispersal resulting from other vectors (e.g. animal transport) is likely to be even harder to predict, and constitutes a daunting task even for a single species. In my view, this problem will always remain, and

will prevent assembly models from achieving the level of precision for which one might otherwise wish.

Beyond difficulties in quantifying dispersal limitation, further unpredictabilities remain. In a series of experimentally created communities which were sown with 20 different species, Weiher and Keddy (1995a) found that although "some aspects of assembly were deterministic", the experiments revealed "an inner lining of inconsistencies and apparently random behaviour". Only about 50% of the species were consistently found within sets of replicates, a result which cannot be attributed to dispersal limitation. This therefore suggests that models of community assembly applied to real communities will offer no more than general guidance as to species composition rather than firm predictions.

8.4 Modelling community assembly

8.4.1 The processes of community assembly

In the foregoing discussion, I have emphasised the fact that it is not enough to know of a species that it can grow under certain environmental conditions to know if it is likely to colonise a community which is subject to those conditions (and from which the species is currently absent). Before we can predict this we must know if it is likely to arrive there (as seeds or spores etc.) in the first place. If propagules arrive in the community, successful colonisation will depend upon how well suited the species is to conditions in the community. If it is very well suited, a single seed may be enough to start a viable population. If it is less well suited, a steady influx of propagules may be necessary to ensure that a viable population continues to flourish (the "mass effect", Schmida and Ellner 1984). The suitability of a species for existence in a community under given environmental conditions may, to a greater or lesser extent, be predicted on the basis of its traits. This stage in community organisation is envisaged here as a series of environmental filters. The

actual organisation of species within the community, however, is a matter of coexistence rather than just existence, and it is in the small-scale spatial organisation of the plants within the community that the effects of competition may most easily be discerned (cf. Menge and Olson 1990). This view of community assembly is illustrated at Figure 8.1.

As a matter of convenience, plant community assembly is portrayed in two stages in Figure 8.1. The same biological processes (e.g. competition and dispersal limitation) may have effects at both stages, but there is an important distinction in the extent to which modelling of the two stages is both desirable and possible. In order to illustrate the principles discussed below, an imaginary situation has been shown. The species pool contains 16 species (S_1 - S_{16}) which are absent from the target community and are divided into five groups. In order to become community members, propagules must first arrive at the community (i.e. 'pass through' the dispersal filter shown at Figure 8.1), before environmental sorting operates on them and they either pass or are prevented from passing through the environmental filters. The width of the species arrows is illustrated as being proportional to the number of dispersed propagules reaching the community for each species over a given period of time. Eight of the 16 species (S_2, S_3, S_5, S_6, S_8, S_9, S_{10} and S_{14}) are shown as passing through the dispersal filter and arriving at the site. These species are then portrayed as being filtered by the environment of the community and different numbers colonise the community as a result of the influence of the environment (e.g. individualistic effects of grazing, soil moisture and nutrient status etc. on the different species). The width of the arrows is proportional to the number of species colonising the community. Of the eight species which dispersed into the community all but one (S_8) are shown as colonising, although in different numbers. Thus the site is shown as receiving many seeds of the two orchids (S_8 and S_9), for example, as may be the case with species which produce prodigious quantities of tiny, widely dispersed seeds. The environment of the site is then shown as exerting a strong filtering effect on the orchids such that one species (S_8) does not colonise the site and the other is present in only small numbers.

The species in a community are not a random selection from those in the species pool as was shown in relation to several of the traits studied in Chapter 3. But in addition to this non-randomness (which can only be detected when the species growing in a community are compared with those which are absent but in theory might be present), there is likely to be further non-randomness in the spatial organisation of the species actually present within the community as discussed above. This is likely to reflect both competition between neighbouring species and other processes such as vegetative spread (Mahdi and Law 1987), localised seed dispersal (e.g. Silvertown and Wilson 1994) and micro-site availability (e.g. Gigon and Leutot 1996, Silvertown and Wilkin 1983, Silvertown 1981) which will tend to create an aggregated distribution of species. It is illustrated in Figure 8.1 as 'stage 2: small scale community organisation' where the diagram might represent an area of vegetation of a few square centimetres. In terms of predicting community composition, there is probably little need to model community assembly at this scale since it is the presence or abundance of species in communities which is the matter of chief concern, rather than their exact spatial arrangements. In any event, predicting the spatial arrangements of species will probably be much harder than even predicting their abundances since, if interspecific competition is a major structuring force, it is hard to see how the spatial arrangement of one species could be predicted without already having knowledge about the spatial organisation of the rest of the community. If, on the other hand, spatial organisation reflects patterns of localised seed dispersal or clonal growth, reliable predictions of small scale patterns will only be possible in a qualitative way. It is, however, at this small scale of

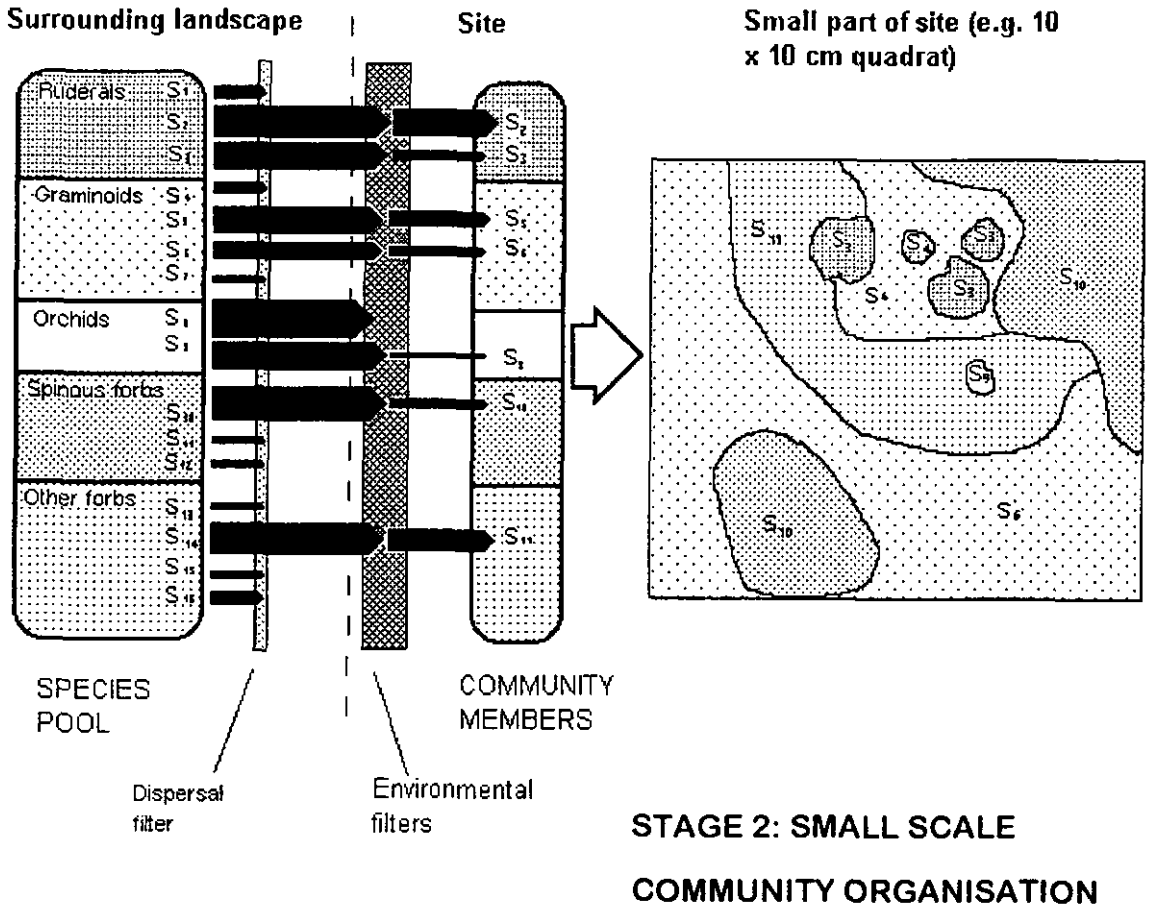


Figure 8.1. Plant community assembly portrayed in two stages, both of which are likely to exhibit non-randomness. On the left is the first stage (species selection), at which species in the species pool are filtered and reduced to a smaller group of species which are present in the community. The first filter is that of *dispersal: species may be absent from a site simply because propagules fail to arrive there.* For those species which arrive at the site, the environment then acts to filter them in various ways by processes and influences such as grazing, soil moisture regime, temperature regime etc. The successful colonists must pass through both sets of filters, and their abundance in the community will depend upon the number of propagules arriving at the site and the likelihood that any propagule will establish and grow. The second stage shows the small-scale organisation of species. The pattern exhibited here is likely to reflect both competition between neighbouring species and clumped distributions resulting from vegetative spread and localised seed dispersal. See text for more details.

community organisation that evidence for plant community assembly rules has often been sought in the field (e.g. Wilson and Watkins 1994).

The species of the species pool have been subdivided into groups in Figure 8.1. This is to emphasise the point that species occurrence may best be predicted by different models depending on what sorts of species are being considered, as suggested in Chapter 3. Species may best be grouped into functional types or guilds for example (e.g. 'ruderals' or 'spinous forbs'). Good powers of seed dispersal may perhaps be very important in the case of short-lived ruderal species in the community but much less so in the longer-lived and more competitive matrix species, as has been suggested by models (Schmida and Ellner 1984, Tilman 1994, Hurtt and Pacala 1995) and empirically (Grubb 1982). For perennial grasses, however, competitive ability or relative growth rate may be better predictors of which species are most likely to occur in a particular community. Models of assembly for the various guilds or functional groups may therefore be quite different. Additionally, different models may best be applied to discrete taxonomic groups (e.g. "orchids"). It is not possible to assess the extent to which phylogeny affects the efficiency of assembly rules on the basis of the work reported in this thesis: every effort was made to eliminate the phylogenetic component in both the large-scale study (Chapter 3) and the subsequent experimental studies for the reasons stated in Chapter 3. But it is quite conceivable that, within particular species groups, different traits have different effects on species performance, over and above any differences due to membership of different guilds or functional groups.

8.4.2 Predictive models of community assembly

Community assembly models fall into two broad types: those which predict which species from the species pool will be present in a community (a simple presence/absence prediction) and those which attach a probability to species occurrence (or attempt to predict species abundance or rank abundance, perhaps linked to occurrence probabilities).

The presence/absence models may be useful in modelling plant community assembly in cases where the ecosystem is a simple one and success of establishment is governed by a few easily understood factors. This was the case in the study by van der Valk (1981), in which a few wetland variables controlled community assembly in a straightforward way. Even in relatively simple environments however, a substantial degree of unpredictability may be present, as suggested by the experimental findings of Weiher and Keddy (1995a).

In general, the situation will be worse from the point of view of modelling community assembly. Most real environments are more complex than those studied be van der Valk or created by Weiher and Keddy (*op. cit.*). Under these circumstances, a model which predicts presence or absence is likely to result in an unacceptably large number of wrong predictions as argued in Chapter 3. For this reason I believe that the most appropriate models for plant community assembly will be those that attach a probability to species occurrence which may be linked to species abundance or rank abundance in the community as attempted in Chapter 3. Even using a simple linear model such as was used in Chapter 3, better results may perhaps be achieved if the species are initially arranged into groups as suggested in Chapter 3 and discussed above.

8.5 Future work and general conclusions

Key tasks for future work include the search for answers to the following questions:

- How predictable is community assembly, and how does this predictability vary between communities?
- Will it be possible to predict species abundances in communities rather than just rank abundances?
- What are the best techniques for modelling the assembly process?
- What is the best way of achieving generality in assembly models: should traits be used, species organised into guilds etc.?
- Does the application of separate assembly rules to different guilds, taxonomic groups of species etc. lead to better predictions, and if so, how should the groups be defined?

Due to modelling difficulties, problems in obtaining trait data and the stochasticity of nature, a high degree of uncertainty is likely to be attached to the predictions of assembly rules. The coarser the scale of prediction and the simpler the environment, the more community assembly lends itself to modelling. At present we have little to guide us in deciding whether a predictive model is a good one or not, because we do not know how intrinsically predictable community assembly is. The results of Chapters 4 and 5 suggest that the study community is not saturated with species (cf. Caley and Schluter 1997). This implies that some species which are able to flourish as community members are actually absent and even if it were possible accurately to assess their suitability for growth in a particular community, their presence in it may be unpredictable. The predictability or otherwise of community assembly can only be assessed by attempting different approaches

to a wide range of communities, preferably coupled with studies of experimentally created communities. There is undoubtedly much more scope for work here.

The use of assembly models in species introduction programmes is worthy of consideration. A model which predicts the likelihood of species occurrence may, for example, be useful for the identification of species which appear to be suitable to growth under certain conditions (but are currently absent). Such species would be potential candidates for introduction if a conservation objective is to increase the species-richness of a site.

I am hopeful that, at least for some environments, it may be possible to model community assembly in a way which is sufficiently precise as to offer useful guidance in environmental decision making. But the science of community assembly is unlikely ever to be an exact one.

References

Aarssen, L.W. (1984). On the distinction between niche and competitive ability: implications for coexistence theory. *Acta Biotheoretica*, **33**, 67-83.

Ackerly, D.D. and Donoghue, M.J. (1995). Phylogeny and ecology reconsidered. *Journal of Ecology*, **83**, 730 - 733.

Ackerman, J.D., Sabat, A. and Zimmerman, J.K. (1996). Seedling establishment in an epiphytic orchid: an experimental study of seed limitation. *Oecologia*, **106**, 192-198.

Armstrong, D.P. and Westoby, M. (1993). Seedlings from large seeds tolerate defoliation better: a test using phylogenetically independent contrasts. *Ecology*, **74**, 1092 - 1100.

Bakker, J.P. (1989). *Nature Management by Grazing and Cutting.* Kluwer Academic Publishers.

Berkefeld, K. (1988). Investigations about ecotype formation in *Galium aparine* L. (*Rubiaceae*) and *Lapsana communis* L. (*Compositae*). *Flora*, **181**, 111-130.

Boutin, C. and Keddy, P.A. (1993). A functional classification of wetland plants. *Journal of Vegetation Science*, **4**, 591-600.

Bowers, M.A. and Brown, J.H. (1982). Body size and coexistence in desert rodents: chance or community structure? *Ecology*, **63**, 391-400.

Bremer, K. (1994). *Asteraceae: Cladistics and Classification.* Timber Press.

Bullock, J.M., Clear Hill, B., Dale, M.P. and Silvertown, J. (1994). An experimental study of the effects of sheep grazing on vegetation change in a species-poor grassland and the role of seedling recruitment into gaps. *Journal of Applied Ecology*, **31**, 493-507.

Bullock, J.M., Clear Hill, B. , Silvertown, J. and Sutton, M. (1995). Gap colonization as a source of grassland community change: effects of gap size and grazing on the rate and mode of colonization by different species. *Oikos*, **72**, 273 - 282.

Burke, M.J.W. and Grime, J.P. (1996). An experimental study of plant community invasibility. *Ecology*, **77**, 776-790.

Caley, M.J. and Schluter, D. (1997). The relationship between local and regional diversity. *Ecology*, **78**, 70-80.

Caputo, P. and Cozzolino, S. (1994). A cladistic analysis of Dipsacaceae (Dipsacales). *Plant Systematics and Evolution*, **189**, 41 - 61.

Chappill, J.A. (1995). Cladistic analysis of the Leguminosae: the development of an explicit phylogenetic hypothesis. In: M. Crisp and J.J. Doyle (eds.). *Advances in Legume Systematics 7: Phylogeny*, pp. 1 - 9. Royal Botanic Gardens, Kew.

Chase, M.W., Soltis, D.E,, Olmstead, R.G., Morgan, D., Les, D.H., Mishler, B.D., Duvall, M.R., Price, R.A., Hills, H.G., Qui, Y.L., Kron, K.A., Rettig, J.H., Conti, E., Palmer, J.D., Manhart, J.R., Sytsma, K.J., Michaels, H.J., Kress, W.J., Karol, K.G., Clark, W.D., Hedrén, M., Gaut, B.S., Jansen, R.K., Kim, K.J., Wimpee, C.F., Smith, J.F., Furnier, G.R., Strauss, S.H., Xiang, Q.Y., Plunkett, G.M., Soltis, P.S., Swensen, S.M., Williams, S.E., Gadek, P.A., Quinn, C.J., Eguiarte, L.E., Golenberg, E., Learn, G.H. Jr., Graham, S.W., Barrett, S.C.H., Dayanandan, S. and Albert, V.A. (1993). Phylogenetics of seed plants: and analysis of nucleotide sequences from the plastid gene *rbc*L. *Annals of the Missouri Botanic Garden*, **80**, 528-580.

Clapham, A.R., Tutin, T.G. and Moore, D.M. (1987). *Flora of the British Isles.* Cambridge University Press.

Cody, M.L. (1978). Distribution ecology of Haplopappus and Chrysothamnus in the Mojave Desert I. Niche position and niche shifts on north-facing granitic slopes. *American Journal of Botany*, **65**, 1107-1116.

Cody, M.L. (1991). Niche theory and plant growth form. *Vegetatio*, **97**, 39-55.

Connor, E.F. and Simberloff, D. (1979). The assembly of species communities: chance or competition? *Ecology*, **60**, 1132-1140.

Cornell, H.V. and Karlson, R.H. (1996). Species richness of reef-building corals determined by local and regional processes. *Journal of Animal Ecology*, **65**, 233-241.

Darwin, C. (1902). *The Origin of Species* (6th Edition). John Murray.

Davis, B.N.K., Lakhani, K.H., Brown, M.C. and Park, D.G. (1985). Early seral communities in a limestone quarry: an experimental study of treatment effects on cover and richness of vegetation. *Journal of Applied Ecology*, **22**, 473-490.

Diamond, J.M. (1975). Assembly of species communities. In: Cody, M.L. and Diamond, J.M. (Eds). *Ecology and Evolution of Communities*. Belknap Press.

Diamond, J.M. and Gilpin, M.E. (1982). Examination of the "null" model of Connor and Simberloff for species co-occurrences on islands. *Oecologia*, **52**, 64-74.

Diaz, S., Acosta, A. and Cabido, M, (1992). Morphological analysis of herbaceous communities under different grazing regimes. *Journal of Vegetation Science*, **3**, 689-696.

Dobson, A.J. (1990). *An Introduction to Generalized Linear Models*. Chapman and Hall.

Downie, S.R. and Katz-Downie D.S. (1996). A molecular phylogeny of Apiaceae subfamily Apioideae: evidence from nuclear ribosomal DNA internal transcribed spacer sequencies. *American Journal of Botany*, **83**, 234 - 251.

Doyle, J.J. (1995). DNA data and legume phylogeny: a progress report. In: M. Crisp and J.J. Doyle (eds.). *Advances in Legume Systematics 7: Phylogeny*, pp. 11 - 30. Royal Botanic Gardens, Kew.

Drake, J.A. (1990). Communities as assembled structures: do rules govern pattern? *Trends in Ecology and Evolution*, **5**, 159-164.

Dyke, G.V. and Patterson, H.D. (1952). Analysis of factorial arrangements when the data are proportions. *Biometrics*, **8**, 1-12.

Ehmann, W.J. and MacMahon, J.A. (1996). Initial tests for priority effects among spiders that co-occur on sagebrush shrubs. *The Journal of Arachnology*, **24**, 173-185.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. and Paulißen, D. (1991). Zeigerwerte von Pflantzen in Mitteleuropa. *Scripta Geobotanica*, **18**, 1 - 248.

Eriksson, O. (1993). The species-pool hypothesis and plant community diversity. *Oikos*, **68**, 371-374.

Eriksson, O. and Ehrlén, J. (1992). Seed and microsite limitation of recruitment in plant populations. *Oecologia*, **91**, 360 - 364.

Felsenstein, J. (1985). Phylogenies and the comparative method. *The American Naturalist*, **125**, 1-15.

Fenner, M. (1987). Seedlings. *New Phytologist*, **106**, 35-47.

Fisher, R.A. (1936). The use of multiple measurements in taxonomic problems. *Annals of Eugenics*, **7**, 179-188.

Fowler, N.L. (1990). Disorderliness in plant communities: comparisons, causes and consequences. In: Grace, J.B. and Tilman, D. *Perspectives on Plant Competition.* Academic Press.

Fox, B.J. and Brown, J.H. (1993). Assembly rules for functional groups in North American desert rodent communities. *Oikos*, **67**, 358-370.

Fox, B.J. and Brown, J.H. (1995). Reaffirming the validity of the assembly rule for functional groups or guilds: a reply to Wilson. *Oikos*, **73**, 125-132.

Gigon, A. and Leutert, A. (1996). The dynamic keyhole-key model of coexistence to explain diversity of plants in limestone and other grasslands. *Journal of Vegetation Science*, 7, 29-40.

Gitay, H. and Noble, I.R. (1997). What are functional types and how should we seek them? In: Smith, T.M., Shugart, H.H. and Woodward, F.I. (eds.). *Plant Functional Types*. Cambridge University Press.

Gotelli, N.J. and Graves, G.R. (1996). *Null Models in Ecology*. Smithsonian Institution Press.

Grace, J.B. (1993). The effects of habitat productivity on competition intensity. *Trends in Ecology and Evolution*, **8**, 229-230.

Grime, J.P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, **111**, 1169 - 1194.

Grime, J.P., Hodgson, J.G. and Hunt, R. (1988). *Comparative Plant Ecology*. Unwin Hyman.

Grime, J.P., Hodgson, J.G., Hunt, R., Thompson, K., Hendry, G.A.F., Campbell, B.D., Jalili, A., Hillier, S.H., Diaz, S. and Burke, M.J.W. (1997a). Functional types: testing the concept in Northern England. In: Smith, T.M., Shugart, H.H. and Woodward, F.I. (eds.). *Plant Functional Types*. Cambridge University Press.

Grime, J.P., Thompson, K., Hunt, R., Hodgson, J.G., Cornelissen, J.H.C., Rorison, I.H., Hendry, G.A.F., Ashenden, T.W., Askew, A.P., Band, S.R., Booth, R.E., Bossard, C.C., Campbell, B.D., Cooper, J.E.L., Davison, A.W., Gupta, P.L., Hall, W., Hand, D.W., Hannah, M.A., Hillier, S.H., Hodkinson, D.J., Jalili, A., Liu, Z., Mackey, J.M.L., Matthews, N., Mowforth, M.A., Neal, A.M., Reader, R.J., Reiling, K., Ross-Fraser, W., Spencer, R.E., Sutton, F., Tasker, D.E., Thorpe, P.C. and Whitehouse, J. (1997b). Integrated screening validates primary axes of specialisation in plants. *Oikos*, **79**, 259-281.

Grubb, P.J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, **52**, 107-145.

Grubb, P.J. (1982). Control of relative abundance in roadside *Arrhenatheretum*: results of a long-term garden experiment. *Journal of Ecology*, **70**, 845-861.

Haefner, J.W. (1978). Ecosystem assembly grammars: generative capacity and empirical adequacy. *Journal of Theoretical Biology*, **73**, 293-318.

Haefner, J.W. (1981). Avian community assembly rules: the foliage gleaning guild. *Oecologia*, **50**, 131-142.

Hanley, M.E., Fenner, M. and Edwards, P.J. (1995). An experimental field study of the effects of mollusc grazing on seedling recruitment and survival in grassland. *Journal of Ecology*, **83**, 621-627.

Harvey, P.H. and Pagel, M.D. (1991). *The Comparative Method in Evolutionary Biology.* Oxford University Press.

Hawkes, J.C., Pyatt, D.G. and White, I.M.S. (1997). Using Ellenberg indicator values to assess soil quality in British forests from ground vegetation: a pilot study. *Journal of Applied Ecology*, **34**, 375-387.

Hendry, G.A. and Grime, J.P. (1993). *Methods in Comparative Plant Ecology: a Laboratory Manual.* Chapman and Hall.

Herrera, C.M. (1992). Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in Mediterranean woody plants. *The American Naturalist*, **140**, 421-446.

Herrera, J. (1991). Herbivory, seed dispersal, and the distribution of a ruderal plant living in a natural habitat. *Oikos*, **62**, 209-215.

Hodgson, J.G., Grime, J.P., Hunt, R. and Thompson, K. (1995). *The Electronic Comparative Plant Ecology*. Chapman and Hall.

Hongo, A. (1989). Transplant survival of *Rumex obtusifolius* L. and *Rumex crispus* L. in three old reseeded grasslands. *Weed Research*, **29**, 13-19.

Houssard, C. and Escarré, J. (1995). Variation and covariation among life-history traits in *Rumex acetosella* from a successional old-field gradient. *Oecologia*, **102**, 70-80.

Hsiao, C., Chatterton, N.J., Asay, K.H. and Jensen, K.B. (1995). Molecular phylogeny of the Pooideae (Poaceae) based on nuclear rDNA (ITS) sequences. *Theoretical and Applied Genetics*, **90**, 389 - 398.

Hulme, P.E. (1994). Post dispersal seed predation in grassland - its magnitude and sources of variation. *Journal of Ecology*, **82**, 645-652.

Hurtt, G,C. and Pacala, S.W. (1995). The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology*, **176**, 1-12.

Jansen, R.K., Holsinger, K.E., Michaels, H.J. and Palmer, J.D. (1990). Phylogenetic analysis of chloroplast DNA restriction site data at higher taxonomic levels: an example from the Asteraceae. *Evolution*, **44**, 2089 - 2105.

Johansson, M.E. and Keddy, P.A. (1991). Intensity and asymmetry of competition between plant pairs of different degrees of similarity: an experimental study on two guilds of wetland plants. *Oikos*, **60**, 27-34.

Keddy, P.A. (1992). Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*, **3**, 157-164.

Kelly, C.K. (1996). Identifying plant functional types using floristic data bases: ecological correlates of plant range size. *Journal of Vegetation Science*, **7**, 417-424.

Kent, D.H. (1992). *List of Vascular Plants of the British Isles*. BSBI.

Kent, D.H. (1996). *List of Vascular Plants of the British Isles: Supplement 1*. BSBI.

Kindscher, K. and Wells, P.V. (1995). Prairie plant guilds: a multivariate analysis of prairie species based on ecological and morphological traits. *Vegetatio*, **117**, 29-50.

Kitajima, K. and Tilman, D. (1996). Seed banks and seedling establishment on an experimental productivity gradient. *Oikos*, **76**, 381-391.

Klinkhamer, P.G.L., de Jong, T.J. and Heiden, L.H. (1996). An eight year study of population dynamics and life-history variation of the "biennial" *Carlina vulgaris*. *Oikos*, **75**, 259-268.

Krzanowski, W.J. (1988). *Principles of Multivariate Analysis*. Clarendon Press, Oxford.

Law, R. and Morton, D. (1996). Permanence and the assembly of ecological communities. *Ecology*, **77**, 762-775.

Leishman, M. and Westoby, M (1992). Classifying plants into groups on the basis of associations of individual traits - evidence from Australian semi-arid woodlands. *Journal of Ecology*, **80**, 417-424.

Leishman, M.R. and Westoby, M. (1994a). The role of seed size in seedling establishment in dry soil conditions - experimental evidence from semi-arid species. *Journal of Ecology*, **82**, 249 - 258.

Leishman, M.R. and Westoby, M. (1994b). Hypotheses on seed size: tests using the semiarid flora of western New South Wales, Australia. *American Naturalist*, **143**, 890-906.

Losos, J.B. (1996). Phylogenetic perspectives on community ecology. *Ecology*, **77**, 1344 - 1354.

Lousley, J.E. and Kent, D.H. (1981). *Docks and Knotweeds of the British Isles.* Botanical Society of the British Isles. London.

Mabberley, D.J. (1990). *The Plant Book.* Cambridge University Press.

Mahdi, A. and Law, R. (1987). On the spatial organization of plant species in a limestone grassland community. *Journal of Ecology*, **75**, 459-476.

Manly, B.F.G. (1991). *Randomization and Monte Carlo methods in biology.* Chapman and Hall, London.

Mann, L.K. and Shugart, H.H. (1983). Discriminant analysis [of] some east Tenessee forest herb niches. *Vegetatio*, **52**, 77-89.

McCullagh, P. and Nelder, J.A. (1989). *Generalized Linear Models.* Chapman and Hall.

McGraw, J.B. and Chapin, F.S. (1989). Competitive ability and adaptation to fertile and infertile soils in two *Eriophorum* species. *Ecology*, **70**, 736-749.

McIntyre, S., Lavorel, S. and Tremont, R.M. (1995). Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. *Journal of Ecology*, **83**, 31-44.

McKendrick, S.L. (1996). The effects of fertilizer and root competition on seedlings of *Orchis morio* and *Dactylorhiza fuchsii* in chalk and clay soil. *New Phytologist*, **134**, 335-342.

Mead, R. and Curnow, R.N. (1983). *Statistical Methods in Agriculture and Experimental Biology*. Chapman and Hall.

Menge, B.A. and Olson, A.M. (1990). Role of scale and environmental factors in regulation of community structure. *Trends in Ecology and Evolution*, **5**, 52-57.

Mitchley, J. (1988). Control of relative abundance of perennials in chalk grassland in southern England. II. Vertical canopy structure. *Journal of Ecology*, **76**, 341 - 350.

Montalvo, J., Casado, M.A., Levassor, C. and Pineda, F.D. (1991). Adaptation of ecological systems: compositional patterns of species and morphological and functional traits. *Journal of Vegetation Science*, **2**, 655-666.

Moyle, P.B. and Light, T. (1996). Biological invasions of fresh water: empirical rules and assembly theory. *Biological Conservation*, **78**, 149-161.

Noble, I.R. (1987). The role of expert systems in vegetation science. *Vegetatio*, **69**, 115-121.

Noble, I.R. and Slatyer, R.O. (1980). The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbance. *Vegetatio*, **43**, 5-21.

O'Connor, I. and Aarssen, L.W. (1987). Species association patterns in abandoned sand quarries. *Vegetatio*, **73**, 101-109.

Olff, H., Pegtel, D.M., van Groendael, J.M. and Bakker, J.P. (1994). Germination strategies during grassland succession. Journal of Ecology, 82, 69-77.

Oliveira Silva, M.T. (1992). Effects of mollusc grazing on the development of grassland species. *Journal of Vegetation Science*, **3**, 267-270.

Osunkoya, O.O., Ash, J.E., Hopkins, M.E. and Graham, A.W. (1994). Influence of seed size and seedling ecological attributes on shade-tolerance of rain-forest tree species in northern Queensland. *Journal of Ecology*, **82**, 149 - 163.

Pärtel, M., Zobel, M., Zobel, K. and van der Maarel (1996). The species pool and its relation to species richness: evidence from Estonian plant communities. *Oikos*, **75**, 111 - 117.

Perring, F.H. and Walters, S.M. (1962) *Atlas of the British Flora.* BSBI, London.

Pillay, M. and Hilu, K.W. (1995). Chloroplast-DNA restriction site analysis in the genus *Bromus* (Poaceae). *American Journal of Botany*, **82**, 239 - 249.

Plunkett, G.M., Soltis, D.E., Soltis, P.S. and Brooks, R.E. (1995). Phylogenetic relationships between Juncaceae and Cyperaceae: insights from *rbc*L sequence data. *American Journal of Botany*, **82**, 520 - 525.

Plunkett, G.M., Soltis, D.E. and Soltis, P.S. (1996). Higher level relationships of Apiales (Apiaceae and Araliaceae) based on phylogenetic analysis of *rbc*L sequences. *American Journal of Botany*, **83**, 499 - 515.

Poff, N.L. (1997). Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society*, **16**, 391-409.

Prentice, H.C. and Cramer, W. (1990). The plant community as a niche bioassay: environmental correlates of local variation in *Gypsophila fastigiata*. *Journal of Ecology*, **78**, 313-325.

Primack, R.B. and Miao, S.L. (1992). Dispersal can limit local plant distribution. *Conservation Biology*, **6**, 513 - 519.

Purvis, A. and Rambaut, A. (1995). Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Computer Appl. Biosciences*, **11**, 247 - 251.

Rabinowitz, D., Rapp, J.K., Cairns, S. and Mayer, M. (1989). The persistence of rare prairie grasses in Missouri: environmental variation buffered by reproductive output of sparse species. *American Naturalist*, **134**, 525-544.

Raunkiaer, C. (1934). *The Life Forms of Plants and Statistical Plant Geography*. Clarendon Press, Oxford.

Read, A.F. and Nee, S. (1995). Inference from binary comparative data. *Journal of Theoretical Biology*, **173**, 99 - 108.

Rees, M. (1996). Evolutionary ecology of seed dormancy and seed size. *Philosophical Transactions of the Royal Society of London* B, **351**, 1299 - 1308.

Rejmánek, M. (1996). A theory of seed plant invasiveness: the first sketch. *Biological Conservation*, **78**, 171-181.

Rich, T.G.C. and Smith, P.A. (1996). Botanical recording, distribution maps and species frequency. *Watsonia*, **21**, 155 - 167.

Richards, C., Haro, R.J., Johnson, L.B. and Host, G.E. (1997). Catchment and reach-scale properties as indicators of macroinvertebrate species traits. *Freshwater Biology*, **37**, 219-230.

Richardson, D.M., Cowling, R.M., Lamont, B.B. and van Hensbergen, H.J. (1995). Coexistence of Banksia species in southwestern Australia: the role of regional and local processes. *Journal of Vegetation Science*, **6**, 329-342.

Rodwell, J.S. (1992). *British Plant Communities. Volume 3: Grasslands and Montane Communities.* Cambridge University Press.

Saverimuttu, T. and Westoby, M. (1996). Seedling longevity under deep shade in relation to seed size. *Journal of Ecology*, **84**, 681-689.

Scarsbrook, M.R. and Townsend, C.R. (1993). Stream community structure in relation to spatial and temporal variation: a habitat templet study of two contrasting New Zealand streams. *Freshwater Biology*, **29**, 395-410.

Schimper, A.F.W. (1903). *Plant-Geography upon a Physiological Basis* (Trans. W.A. Fisher). Clarendon Press, Oxford.

Schmida, A. and Ellner, S. (1984). Coexistence of plant species with similar niches. *Vegetatio*, **58**, 29-55.

Silvertown, J. and Law, R. (1987). Do plants need niches? Some recent developments in plant community ecology. *Trends in Ecology and Evolution*, **2**, 24-26.

Silvertown, J. and Smith, B. (1989). Germination and population structure of spear thistle *Cirsium vulgare* in relation to experimentally controlled sheep grazing. *Oecologia*, **81**, 369-373.

Silvertown, J. and Wilson, J.B. (1994). Community structure in a desert perennial community. *Ecology*, **75**, 409-417.

Silvertown, J. and Wilkin, F.R. (1983). An experimental test of the role of micro-spatial heterogeneity in the co-existence of congeneric plants. *Biological Journal of the Linnean Society*, **19**, 1-8.

Silvertown, J., Watt, T.A., Smith, B. and Treweek, J.R. (1992). Complex effects of grazing treatment on an annual in a species-poor grassland community. *Journal of Vegetation Science*, **3**, 35-40.

Smith, T.M., Shugart, H.H. and Woodward, F.I., eds. (1997). *Plant Functional Types.* Cambridge University Press.

Stace, C (1991). *New Flora of the British Isles.* Cambridge University Press.

Sterk, A.A., Groenhart, M.C. and Mooren, J.F.A. (1983). Aspects of the ecology of some microspecies of *Taraxacum* in the Netherlands. *Acta Botanica Neerlandica*, **32**, 385-415.

Stone, L., Dayan, T. and Simberloff, D. (1996). Community-wide assembly patterns unmasked: the importance of species' differing geographical ranges. *The American Naturalist*, **148**, 997-1015.

Susanna, A., Jacas, N.G., Soltis, D.E. and Soltis, P.S. (1995). Phylogenetic relationships in tribe Cardueae (Asteraceae) based on ITS sequences. *American Journal of Botany*, **82**, 1056 - 1068.

Sydes, C.L. (1984). A comparative study of leaf demography in limestone grassland. *Journal of Ecology*, **72**, 331-345.

Thompson, K. and Hodgson, J.G. (1996). More on the biogeography of scarce vascular plants. *Biological Conservation*, **75**, 299-302.

Thompson, K., Hodgson, J.G., Grime, J.P., Rorison, I.H., Band, S.R. and Spencer, R.E. (1993). Ellenberg numbers revisited. *Phytocoenologia*, **23**, 277-289.

Thompson, K., Hillier, S.H., Grime, J.P., Bossard, C.C. and Band, S.R. (1996). A functional analysis of a limestone grassland community. *Journal of Vegetation Science*, **7**, 371-380.

Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology*, **75**, 2-16.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology*, **78**, 81 - 92.

Treweek, J.R. (1990). *The ecology of sheep grazing: its use in nature conservation management of lowland neutral grassland.* Unpublished D. Phil Thesis, Keble College, Oxford.

Treweek, J.R., Watt, T.A. and Hambler, C. (1997). Integration of sheep production and nature conservation: experimental management. *Journal of Environmental Management*, **50**, 193-210.

van der Valk, A.G. (1981). Succession in wetlands: a Gleasonian approach. *Ecology*, **62**, 688-696.

Wagstaff, S.J., Olmstead, R.G. and Cantino, P.D. (1995). Parsimony analysis of cpDNA restriction site variation in subfamily Nepetoideae (Labiatae). *American Journal of Botany*, **82**, 886 - 892.

Wardle, D.A., Nicholson, K.S. and Rahman, A. (1992). Influence of pasture grass and legume swards on seedling emergence and growth of *Carduus nutans* L. and *Cirsium vulgare* L. *Weed Research*, **32**, 119-128.

Watt, T.A,, Treweek, J.R. and Woolmer, F.S. (1996). An experimental study of the impact of seasonal sheep grazing on formerly fertilized grassland. *Journal of Vegetation Science*, **7**, 535-542.

Wedin, D. and Tilman, D. (1993). Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. *Ecological Monographs*, **63**, 199-229.

Weiher, E. and Keddy, P.A. (1995a). The assembly of experimental wetland plant communities. *Oikos*, **73**, 323-335.

Weiher, E. and Keddy, P.A. (1995b). Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos*, **74**, 159-163.

Westerbergh, A. and Nyberg, A. (1995). Selective grazing of hairless *Silene dioica* plants by land gastropods. *Oikos*, **73**, 289-298.

Westoby, M. and Leishman, M. (1997). Categorizing plant species into functional types. In: Smith, T.M., Shugart, H.H. and Woodward, F.I. (eds.). *Plant Functional Types*. Cambridge University Press.

Westoby, M., Leishman, M. and Lord, J. (1996). Comparative ecology of seed size and dispersal. *Philosophical Transactions of the Royal Society of London* B, **351**, 1309 - 1318.

Wilson, J.B. (1994). Who makes the assembly rules? *Journal of Vegetation Science*, **5**, 275-278.

Wilson, J.B. (1995). Null models for assembly rules: the Jack Horner effect is more insidious than the Narcissus effect. *Oikos*, **72**, 139-144.

Wilson, J.B. and Gitay, H. (1995). Community structure and assembly rules in a dune slack: variance in richness, guild proportionality, biomass constancy and dominance/diversity relations. *Vegetatio*, **116**, 93-106.

Wilson, J.B. and Roxburgh, S.H. (1994). A demonstration of guild-based assembly rules for a plant community, and determination of intrinsic guilds. *Oikos*, **69**, 267-276.

Wilson, J.B. and Watkins, A.J. (1994). Guilds and assembly rules in lawn communities. *Journal of Vegetation Science*, **5**, 591-600.

Wilson, J.B. and Whittaker, R.J. (1995). Assembly rules demonstrated in a saltmarsh community. *Journal of Ecology*, **83**, 801-807.

Wilson, J.B., Steel, J.B., Newman, J.E. and Tangney, R.S. (1995a). Are bryophyte communities different? *Journal of Bryology*, **18**, 689-705.

Wilson, J.B., Sykes, M.T. and Peet, R.K. (1995b). Time and space in the community structure of a species-rich limestone grassland. *Journal of Vegetation Science*, **6**, 729-740.

Wilson, J.B., Crawley, M.J., Dodd, M.E. and Silvertown, J. (1996a). Evidence for constraint on species coexistence in the vegetation of the Park Grass experiment. *Vegetatio*, **124**, 183-190.

Wilson, J.B., Wells, T.C.E., Trueman, I.C., Jones, G., Atkinson, M.D., Crawley, M.J., Dodd, M.E. and Silvertown, J. (1996b). Are there assembly rules for plant species abundance? An investigation in relation to soil resources and successional trends. *Journal of Ecology*, **84**, 527-538.

Wilson, J.B., Lines, C.M. and Silvertown, J. (1996c). Grassland community structure under different grazing regimes, with a method for examining species association when local richness is constrained. *Folia Geobotanica et Phytotaxonomica*, **31**, 197-206.

Zobel, M. (1997). The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in Ecology and Evolution*, **12**, 266-269.

Appendix 1

Biological Flora

of

Cirsium eriophorum

Cirsium eriophorum (L.) Scop

Carduus eriophorus L.; *Cnicus eriophorus* (L.) Roth

Sect. *Eriolepis* (Cass.)Dumort. Monocarpic with a thick tap root or poorly branched main roots. Basal leaves to 80 cm, ovate-oblong in outline, narrowing into a short stalk, deeply pinnatifid and strongly undulate, the narrowly lanceolate distant spine-tipped (4-11 mm) segments usually in pairs with the stem-ward lobe directed upwards and apical lobe downwards, lobes 4 - 11 x 0.7 - 2.2 cm with inrolled margins, midrid often purplish (at least towards the stem), leaves somewhat hispid-hairy above, tomentose below. Stem erect, pale green with or without longitudinal purplish streaks in lower part, to 20 mm diameter at base, densely covered with +/- patent hairs to *c.* 6 mm long, unwinged and not prickly, furrowed, 40 - 160(-180) cm, corymbosely branched above. Stem leaves similar to basal, but sessile and loosely auriculate. Capitula (3-)10-50(-61) in number, more or less long-pedunculate and erect, usually with a few small subtending leaves. Involucre 4-7 x 5-7 cm (width x height), usually solitary, very cottony and white; bracts lanceolate-acuminate, innermost 43-46 x 1.5-2 mm, outermost 16-19 x 3-4 mm, ending in a long narrow purplish ciliate point, usually with a slight dilation just below its apex; the outermost spine-tipped. Corolla 2.5-4.5 cm, florets red-purple, anthers purple (see also VIII a). Achenes 3.9-5.4 x 2.0-2.4 x 1.2-1.5 mm, smooth and shiny, buff flecked with short black streaks; pappus of feather-like hairs 15-33 mm long, white, attached to an ochraceous collar.

A very distinctive and striking member of the British flora. On mainland Europe, the species is not always so well defined, with a welter of varieties, subspecies or closely

related species having been described (particularly from the Balkan peninsula, Fl. Eur. **4**). British material is regarded as an endemic subspecies (subsp. *brittanicum* Petrak) by some authors.

In Britain, it is confined to calcareous soils and is commonest on roadsides, rough grassland, pasture and amongst light scrub. It also occurs in woodland clearings and quarries and other disturbed habitats, such as spoil bank and scree habitats created by limestone quarrying (Anderson and Shimwell 1981). In the following account, nomenclature follows Kent (1992).

I. Geographical and altitudinal distribution

As a native species *C. eriophorum* is restricted to western and central Europe, extending northwards to northern England (Teesdale) and (as a casual) in S.E. Scotland, eastwards to Rumania, and to Spain and northern Italy in the south. Its geographical distribution is broadly similar to that of *C. acaule* (Pigott 1968) although *C. eriophorum* extends further to the south-west (being present in Albania, Hungary and Greece), and not so far to the north (being absent from Denmark, Norway, Sweden and Russia). Some authors (e.g. Hegi Fl. **VI. 4.**) state the range of *C. eriophorum* extends into the upper Volga and other parts of Russia (as *C. eriophorum* subsp *decussatum* (Janka) Petrak), but Fl. Eur. **4** treats this taxon as a separate species (*C. decussatum* Janka). The limits of its distribution seem to be set largely by temperature (see II(a)). Records of *C. eriophorum* as an introduced species appear to be few. Thompson (1922) cites a record for New Zealand (the Upper Wairarapa) from 1899, noting it 'has not been recorded since'. Information in Webb *et al.* (1988) suggests, however, that New Zealand records of *C. eriophorum* refer to *C. brevistylum* Cronq..

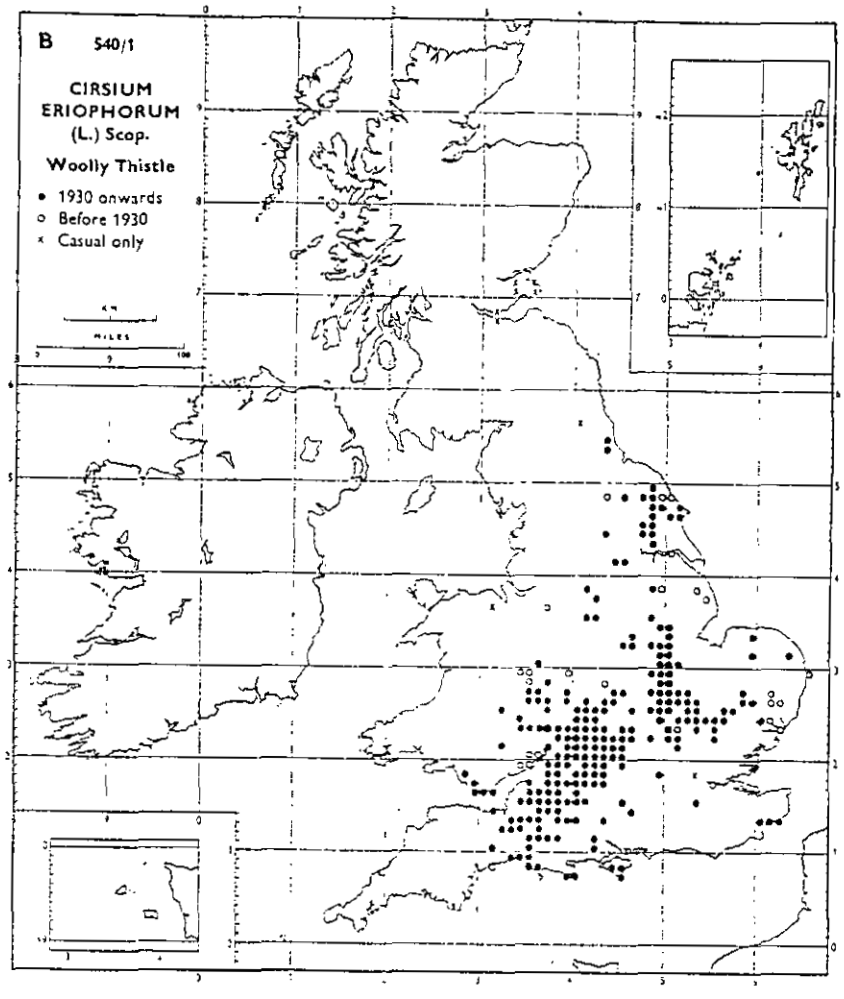


Figure 1. The distribution of *Cirsium eriophorum* in the British Isles.

A record from Turkey also appears to be an error (Davis 1975). Local in England and Wales, and absent from Ireland (Fig. 1), *C. eriophorum* has been recorded as a casual in south-east Scotland for over a century (see e.g. Hooker and Arnott 1860). It appears to have had a restricted distribution since records began. Ray (1724), comparing it with *Cirsium vulgare*, notes '...quo etiam multo rarior est'. It is commoner in the central and western parts of its English range, being probably most abundant in Oxfordshire,

Gloucestershire, Avon and Wiltshire. It is rare in eastern counties such as Essex (Jermyn 1974), Suffolk and Norfolk (Simpson 1982; Petch and Swan 1968; Trist 1979), and Hertfordshire (Dony 1967), and in the north-east such as the Howardian Hills of North Yorkshire (Gulliver 1990). It also becomes scattered in the southern and western extremities of its British range, despite the presence of habitat which appears at least geologically suitable. Perhaps the most puzzling aspect of its British distribution is its scarcity or absence from the North and South Downs, and in this respect it differs markedly from *C. acaule*, another calcicole thistle (see II(a)). In England it has been found at up to 260 m in Yorkshire (Fl. Br. Isl.), and to 270 m at Crickley Hill, Glos and 310 m at Hassop Mines, Derbyshire during the course of the present survey (see Table 1, sites 7 and 10). In continental Europe, it often occurs at higher altitudes and grows at up to 2000 m in Tirol. It is classified as a subalpine species in the north-eastern part of Italy for example (Poldini 1991). *C. eriophorum* appears to be a local species throughout most of its range. It is regarded as one of the rarer thistles in southern Germany, lower Austria and the Alsace by Freese (1995).

II. Habitat

(a) CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

Salisbury (1952) gives the distribution of *C. eriophorum* in England and Wales as oceanic, and contrasts its preference for humid locations here with the species in mainland Europe which is described as continental. Ellenberg *et al.* (1991), however, give the status of *C. eriophorum* in Central Europe as being between oceanic and suboceanic. Its distribution suggests that temperature is important in determining the extent of its overall range. In the British Isles, it becomes scarce or rare in its more northerly stations such as the

limestone areas of the southern Peak District (Linton 1903; Clapham 1969) and in western parts of its range such as the coastal regions of Glamorgan despite the humidity of these areas being greater than that in the core of its distribution in Wiltshire, Gloucestershire and Oxfordshire, and it is completely absent from some apparently suitable oceanic areas such as parts of the south-western coast of Wales and North Wales. It is also absent from the Carboniferous limestone of the Craven in West Yorkshire. It is noted (Hegi Fl. **VI. 4.**) that in its northern stations on mainland Europe, it occurs exclusively on south-facing slopes, and contrasts this with its more central stations in the Alps where it is much less particular in its requirements. This fact is consistent with temperature limitation, and is also seen in *Cirsium acaule*. The rarity or absence of *C. eriophorum* from much of the drier counties of Kent, Sussex and Surrey contrasts with the distribution of *C. acaule*. This aspect of its distribution does not correlate well with low rainfall *per se*, but shows a better correlation with summer water balance (i.e. the difference between rainfall and evaporation), being scarce or absent from areas where an agricultural drought might be expected in more than five summers out of ten (Atlas of Britain & Northern Ireland). The limits to the European distribution of *C. eriophorum* in the north and east appear to be determined by low winter temperature and its north-western limits determined by summer warmth. In Britain it is rare or absent outside the 60^0F (15.6^0C) mean August temperature isotherm (Cl. Atl.). This may account for its absence from Ireland where the summers are cooler. The southern European boundary does, however, suggest that high summer temperatures and drought may restrict its distribution in the Mediterranean region, and its scarcity or absence from much of south-east England may be attributable to a similar cause. In general, the factors limiting its wide-scale distribution appear to be similar to those which constrain *C. acaule*.

(b) SUBSTRATUM

(i) *Solid geology*

In Britain, *C. eriophorum* is restricted to freely-draining base-rich soils over chalk and limestone, the principal rocks in the British Isles being Oolitic Limestone and Chalk, with locally frequent occurrences on the Lias in Somerset and Dorset. It occurs only rarely on the geologically older Carboniferous (e.g. Peak District and the Gower) and Magnesian (North Yorkshire) Limestones. The extent to which it shows a preference for particular limestone types is unclear, due to the extent to which geology is confounded with climate. In the centre of its range in Wiltshire, it occurs most frequently on Oolitic limestone, but is also frequent on the Lower Chalk (Grose 1957). In Dorset near the southern extreme of its British range, it is virtually confined to soils over the Jurassic limestones and almost absent from the abundant chalk (Good 1948). In Staffordshire, *C. eriophorum* is rare on Carboniferous limestone, but frequent on Silurian limestone (Edees 1972). On the continent, it rarely occurs on any other substrate than chalk in the northern part of its range, but it is much more catholic in its southern stations (Hegi Fl. **VI. 4.**). Mannagetta (1892) includes a record from sandstone.

(ii) Surface geology

In Dorset, *C. eriophorum* has mostly been recorded from red-brown rendzinas (Good 1948). In the eastern counties of Suffolk (Simpson 1982) and Cambridgeshire (Perring *et al.* 1964), it is recorded from Boulder Clay. During the course of the survey, *C. eriophorum* was recorded from clay, silty loam, sandy loam or loamy sand topsoils, over

chalk or limestone lumps, with a pH range of 6.7 - 8.1. Its pH range in north-east Italy is given as 5.5 - 8 (Poldini 1991). Hegi (Fl. **VI. 4.**) regards it as showing little soil preference in the southern part of its European range (and Burnat (1931) records it from 'bords des champs silice'), but Hegi (*op. cit.)* does record it from heavy chalk and clay-marl soils and notes that it is nitrophilous. In Central Europe, it is classified as an indicator of relatively dry basic soils and chalk, growing on moderately nitrogen-rich soils (Ellenberg *et al.* 1991).

III. Communities

In Britain, *C. eriophorum* occurs in CG2, CG3 and CG5 grassland communities (Rodwell, 1992), although it is a constant in none. Quadrat data from British localities are given at Table 1.

C. eriophorum occurs most frequently in rough grassland communities, maintained either by periodic grazing or mowing. Typical associates include *Festuca rubra*, *Dactylis glomerata* and, in the roughest swards, *Arrhenatherum elatius*. *C. eriophorum* favours conditions with at least moderate levels of nutrients, and often grows in disturbed areas with species such as *Urtica dioica*. In north Wiltshire it has been described as 'a bane to some farmers' (Gillam 1993) and can behave as a weed in badly managed pastures (e.g. Cherhill Down and Bishopton Down, Wiltshire) where poaching has occurred. In such situations it is associated with *Urtica dioica* and *Cirsium arvense*. Suitable mown habitats are most frequently encountered along roadside verges in the infrequently cut strip furthest from the metalled surface (e.g. close to a hedge or bank). In such circumstances it is often associated with rank grasses such as *Arrhenatherum elatius* and *Elytrigia repens*, tall herb species such as *Heracleum sphondylium*, *Anthriscus sylvestris* and *Rumex* spp., and woody species such as *Rubus caesius* and *R. fruticosus* agg. Along roadsides and in similar

situations, ditch clearance and the associated disturbance to the verge and spreading of soil may also help to provide suitable habitat for *C. eriphorum*. It is also found in incipient scrub communities, and is known as a coppicing plant in Hatfield Forest in Essex (Rackham 1989). It has been recorded from woodland clearings in Oxfordshire (J. Dunn, pers. comm.) and has been recorded from apparently similar situations elsewhere in Europe (e.g. Hayek and Markgraf 1931; Mannagetta 1892). *C. eriophorum* can survive and flower under light shading from scrub.

Less frequently *C. eriophorum* may be found growing amongst species characteristic of acid soils and has been recorded from stands of bracken (Table 1, site 6) in Gloucestershire. Even in such situations, the soil around the roots of *C. eriophorum* appears to be basic. It has been recorded from limestone heath (Horwood and Noel 1933).

In central Europe, *C. eriophorum* is the character species of the ruderal *Cirsietum eriophori* occurring alongside calcareous roadsides and on limestone sheep grazings. It has been recorded from pastured *Seslerietum*, and berberis-rose scrub. A *Cirsium eriophorum* - *Festuca ovina* association is also known (Hegi Fl. **VI. 4.**).

Table 1. Quadrat data (2x2m) for stands containing *Cirsium eriophorum*. Cover expressed on DOMIN scale.

Site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Cirsium eriophorum	5	3	4	4	4	4	6	5	7	5	4	3	5	3	3	3
Achillea millefolium	.	.	3	1	1	.	2	4	.	.	.	3	.	.	3	1
Agrimonia eupatoria	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.
Agrostis capillaris	.	.	.	.	4	4	.	.	1	.	.	.	.	.	.	.
Agrostis gigantea	.	.	.	.	2	.	.	.	4	.	.	.	.	.	3	.
Agrostis stolonifera	.	.	7	3	.	.	.	.	.	.	.	.	4	3	.	.
Anthriscus sylvestris	3	.	.	.	.	.	.	2	.	.	3	2	.	1	3	.
Arenaria seryllifolia	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.
Arrhenatherum elatius	6	4	.	1	4	1	5	7	2	4	8	7	7	4	4	.
Bromus erectus	.	5	.	.	.	.	.	4	.	.	.	.	.	.	.	.
Bromus hordeaceus	.	.	.	.	.	.	1	.	.	.	.	.	.	4	.	.
Campanula rotundifolia	.	1	.	.	.	.	.	.	.	3	.	.	.	.	.	.
Carex flacca	.	2	.	.	.	.	.	.	.	1	.	.	.	.	.	.
Centaurea nigra	.	.	.	2	.	.	.	.	.	.	.	2	4	.	1	4
Centaurea scabiosa	.	.	4	.	.	.	.	3	.	.	.	4	.	.	.	.
Cerastium fontanum	.	.	.	.	1	.	1	.	1	.	.	.	.	.	.	.
Cirsium arvense	1	.	3	1	4	.	.	4	.	.	.	1	.	.	.	4
Cirsium vulgare	.	.	4	1	.	.	.	.	.	.	.	.	.	.	1	.
Clematis vitalba	7	.	.	.	.	.	.	.	.	.	5	.	.	.	.	.
Convolvulus arvensis	.	.	1	.	.	.	.	.	.	.	2	4	3	4	3	.
Crepis capillaris	.	.	.	3	.	.	3	.	2	.	.	.	.	.	.	.
Cynosurus cristatus	.	.	.	.	5	.	.	.	4	.	.	.	.	.	.	.
Dactylis glomerata	3	.	4	4	5	.	4	5	4	4	.	5	4	4	4	3
Elytrigia repens	3	.	.	.	.	.	.	2	.	.	.	5	3	.	4	8
Festuca rubra	.	7	4	8	5	5	7	4	4	6	.	4	.	7	8	.
Fraxinus excelsior (seedling)	.	.	.	.	.	2	.	.	.	.	.	.	.	1	.	.
Galium aparine	1	.	.	.	.	.	.	.	.	.	4	.	.	.	.	1
Galium verum	.	4	.	1	1	.	.	3	.	.	.	.	.	3	.	.
Glechoma hederacea	3	.	.	1	.	.	.	6	.	.	.	.	.	.	.	.
Heracleum sphondylium	5	.	.	.	.	.	.	4	.	.	4	4	.	.	1	.
Holcus lanatus	.	.	3	4	5	2	4	.	3	.	.	.	.	.	.	.
Leontodon hispidus	.	2	.	1	.	.	.	.	1	.	.	.	.	.	.	.
Linum catharticum	.	.	.	.	.	.	.	.	1	3	.	.	.	.	.	.
Lolium perenne	.	.	.	1	5	.	4	.	4	.	.	.	.	3	.	.
Lotus corniculatus	.	4	1	1	.	.	.	.	4	4	.	.	.	.	.	.
Medicago lupulina	.	.	.	.	.	.	.	.	1	3	.	.	2	.	.	.
Phleum bertolonii	.	2	4	4	5	.	2	.	1	.	.	2	4	.	.	.
Pimpinella saxifraga	.	4	.	2	.	.	.	.	.	.	.	.	.	.	.	.
Plantago lanceolata	.	3	2	4	.	3	2	2	4	3	.	.	.	3	.	.
Poa pratensis	.	.	.	.	5	1	.	4	.	.	.	.	.	.	.	.
Poa trivialis	1	.	.	.	.	.	2	.	1	3	.	.	.	.	3	.
Potentilla reptans	.	.	.	.	.	.	.	4	3	.	.	.	3	.	3	.
Ranunculus repens	.	.	1	.	.	.	4	.	1	.	.	.	.	.	.	.
Rubus caesius	3	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.
Rubus fruticosus agg.	.	.	.	.	.	4	.	5	.	4	.	.	.	.	3	.
Sanguisorba minor	.	4	.	2	.	.	4	.	.	4	.	.	.	.	.	.
Scabiosa columbaria	.	1	.	.	.	.	.	.	.	3	.	.	.	.	.	.
Senecio jacobaea	.	1	3	1	.	.	1	.	.	1	.	.	.	.	.	.
Sonchus asper	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Stachys sylvatica	4	.	.	.	.	.	.	.	.	.	.	.	.	.	3	4
Taraxacum agg.	.	.	.	2	.	1	2	.	.	.	.	.	.	1	.	.
Torilis japonica	3	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.
Trifolium pratense	.	.	1	4	2	.	.	.	.	.	.	.	.	3	.	.
Trifolium repens	.	.	2	4	.	4	.	.	4	2	.	2	.	.	.	.
Trisetum flavescens	.	.	1	1	4	.	.	.	4	.	.	.	.	4	.	.
Urtica dioica	3	.	2	.	.	.	1	4	.	.	5	.	.	.	.	4
Veronica chamaedrys	.	3	.	1	2	1	.	.	2	2	.	2	.	.	.	.

See overleaf for key to sites and further details.

Table 1. Cont'd.

1. On top of steep ditch bank, Sharnbrook, Beds (TL0060). Unmanaged, bare ground=0%. Clay soil with limestone chips, pH=8.2. **2.** Beside track, Langdon Hill, Berks (SU5483). Moderate rabbit grazing, bare ground=10%. *Cirsium acaule* 1, *Filipendula vulgaris* 1, *Iberis amara* 1. Clay loam soil with chalk chips, pH=7.6. **3.** Roadside verge, S. of Aston Tyrold, Berks (SU5585). Occasional cutting & vehicle disturbance, bare ground=15%. *Geranium dissectum* 1, *Hypericum perforatum* 1, *Melilotus* sp. 4, *Myosotis arvensis* 1, *Pastinaca sativa* 5, *Plantago major* 1, *Rosa* sp (seedling) 1. **4.** Pasture, Knap Hill, Wilts (SU1263). Light cattle grazing & rabbit grazing, bare ground=3%. *Festuca pratensis* 1, *Ononis spinosa* 3, *Plantago media* 4, *Poa annua* 1, *Primula veris* 1, *Ranunculus bulbosus* 2, *Rumex acetosa* 1, *Senecio vulgaris* 1. Soil pH=7.9. **5.** Pasture, Cherhill Down, Wilts (SU0569). Light summer sheep-grazing, bare ground=0%. Soil pH=7.9. **6.** Bracken-dominated rough ground, Cam Long Down, Glos (ST7799). Unmanaged, bare ground=0%. *Chamerion angustifolium* 4, *Pseudoscleropodium purum* 1, *Crataegus monogyna* (seedling) 1, *Geum urbanum* 1, *Leontodon autumnalis* 3, *Potentilla sterilis* 2, *Pteridium aquilinum* 9, *Ranunculus acris* 1, *Rhytidiadelphus squarrosus* 2, *Viola* sp. 1. Thin layer of sandy soil (Cotteswold Sands) over Inferior Oolite, pH=7.7. **7.** Pasture, Crickley Hill, Glos (SO9316). Rabbit-grazed, also sheep-grazed outside summer season, bare ground=2%. *Geranium pusillum* 2, *Sisymbrium altissimum* 1. Soil mixed with large limestone lumps, pH=7.3. **8.** Roadside verge, Winstone, Glos (SO9709). Light rabbit grazing and occasional cutting, bare ground=0%. *Artemesia vulgaris* 4, *Brachypodium pinnatum* 4, *Knautia arvensis* 3, *Lamium album* 4, *Lathyrus pratensis* 1, *Rosa* sp. (seedling) 2, *Vicia sepium* 1. Light soil with scattered limestone lumps, pH=7.6. **9.** Pasture, Hill End Farm, Oxon (SP4607). Light sheep-grazing all year, moderate cattle-grazing May-October, localised heavy rabbit grazing, bare ground=0%. *Bellis perennis* 1, *Brachythecium rutabulum* 2, *Leontodon taraxacoides* 1. Fine sandy soil, pH=8.5. **10.** Rough grassland, Hassop Mines Derbys (SK2273). Light rabbit grazing, bare ground = 0%. *Briza media* 3, *Euphrasia confusa* 3, *Geranium molle* 1, *Helianthemum nummularium* 5, *Koeleria macrantha* 2, *Potentilla erecta* 1. Fine black soil over limestone, pH=7.3. **11.** Rough grassland, Croughton, Northants (SP5633). Unmanaged, bare ground=0%. Sandy clay with a few limestone chips, pH=7.9. **12.** Roadside verge, Fairford, Glos (SP1601). Occasionally mown, bare ground=0%. *Allium vineale* 3, *Carex spicata* 3. Sandy silt loam with limestone lumps, pH=7.8. **13.** Rough grassland, Stanford Hall, Lechlade, Glos (SP1802). Unmanaged, bare ground=0%. *Ononis repens* 3, *Vicia sativa* ssp. *nigra* 3. Loamy sand with limestone chips, pH=7.7. **14.** Rough grassland, Little Wittenham, Oxon (SU5692). Sheep grazing outside summer season, bare ground=5%. *Hordeum secalinum* 4, *Odontites verna* 3. Silt loam with small chalk chips, pH=8.1. **15.** Roadside verge, Wick, Glamorgan (SS9172). Occasionally mown, bare ground=0%. *Dipsacus fullonum* 4, *Eurhynchium praelongum* 3, *Rumex sanguineus* 3. Sandy loam over limestone lumps, pH=7.7. **16.** Rough grassland on roadside bank, Cardiff (ST1077). Unmanaged, bare ground=0%. *Eupatorium cannabinum* 3, *Rumex crispus* 1, *Tussilago farfara* 4. Silty loam, pH=7.6.

IV. Response to biotic factors

(a) GRAZING

The mature leaves of *C. eriphorum* are protected by stiff sharp spines, and are unpalatable to most stock. The abundance of this species (and other members of the *Onopordion*) around central European villages in which cattle and sheep are still driven is attributed to the fact that mature plants are avoided by grazing animals (Ellenberg 1986). When present in hay, *C. eriophorum* is avoided by cattle although *Cirsium arvense* is much favoured (D. Millin, pers. comm.). The first few (typically 5 - 6) true leaves are, however, only softly spined, and such leaves are eaten with relish by sheep. In comparison with *C. vulgare*, the young leaves of *C. eriophorum* are softer, less hispid, longer and more erect in habit, and these factors conspire to make *C. eriophorum* more susceptible to grazing damage in the early stages. In such circumstances, repeated grazing of small *C. eriophorum* plants may lead to much reduced numbers or elimination from a community. Observations in various parts of England (Gloucestershire, Bedfordshire, Berkshire and Wiltshire) show both *C. eriophorum* and *C. vulgare* to be present in lightly managed (cut or grazed) grassland, but only *C. vulgare* to be present in adjacent and closely grazed agricultural grasslands. *C. eriophorum* may grow on downland on disturbed soil around rabbit warrens (e.g. Knap Hill, Wiltshire - Table 1, site 4), and in such situations it appears to be avoided by rabbits. During the course of fieldwork undertaken for this study, the site where *C. eriophorum* was found in greatest profusion (Hill End Farm, Oxfordshire - Table 1, site 9) showed evidence of heavy rabbit activity. Light sheep grazing occurred throughout the year, with moderate cattle grazing from May to October. *C. eriophorum* is controlled at this site by means of cutting and removing about 80% of all flowering plants each year, resulting in a relatively stable but high population (up to 45 plants in a 10 x 10 m quadrat).

(b) OTHER PLANTS

Performance in the early stages of growth is greater in areas of bare soil compared with vegetated ground. This result is similar to that for *C. vulgare*, although in a comparative experiment at Little Wittenham, Oxfordshire, seeds of *C. eriophorum* planted into a sheep-grazed sward showed significantly better establishment (up to the two true-leaf stage) than those of *C. vulgare* (up to 76% survival *vs.* 13% respectively), despite their percentage germination of both species in the laboratory being identical. Once established, the surrounding vegetation probably has relatively little effect on plants of *C. eriophorum* other than to slow their growth except where the vegetation causes shading; the rosettes are large (up to 1.6m diameter), and have the capacity to weaken or kill the surrounding plants over which the rosette leaves spread. This response is probably not due to the effects of shading alone, but also caused by the positive pressure exerted by the rosette leaves on the surrounding vegetation and ground (Salisbury 1952). The upper part of the leaf stalk grows at a greater rate than the lower, apparently caused by the combined stimuli of gravity and high light intensity operating on the growth hormones (Salisbury *op. cit.*).

V. Response to environment

(a) GREGARIOUSNESS

Almost invariably moderately to highly gregarious in Britain over a scale of a few tens of metres. *C. eriophorum* is also reported as gregarious on mainland Europe (Hegi Fl. **VI. 4.**, Ellenberg *et al.* 1991). Plants usually occur in groups of a few individuals in suitable areas of grassland, often where some obvious disturbance has occurred (e.g. old rabbit scrapes).

(b) PERFORMANCE IN VARIOUS HABITATS

Observations suggest that *C. eriophorum* is more prolific in areas which are ungrazed or only lightly grazed during the early stages of establishment, although a closed sward reduces the number of individuals germinating and surviving through the early stages. The species is therefore most abundant where some form of disturbance has created suitable germination sites in a grassland (e.g. rabbit scrapes, poaching by stock) after which the disturbance regime has been relaxed to allow establishment. *C. eriophorum* is occasionally found in light scrub and woodland clearings. It favours conditions of high light intensity, and only exceptionally occurs where shading reduces light levels to 40% of the amount received in unshaded conditions (Ellenberg *et al.* 1991). It seldom occurs under mown conditions except where mowing is very infrequent (once every few years), although plants which are cut in the spring immediately prior to stem elongation are able to produce (relatively small) flowering stems later in the same year.

(c) EFFECT OF FROST, DROUGHT, ETC.

The rosettes of *C. eriophorum* are (to some extent) winter-green, at least in southern England, although the large, distant-lobed leaves of the previous autumn die off during hard weather, and the only evidence of the thistle is a small rosette of short, closely-lobed leaves of a few centimetres in length. This small rosette is often inconspicuous, and typically covered by the surrounding vegetation. Ellenberg *et al.* (1991) classify *C. eriophorum* as a summer-green species. It develops a substantial root, and larger plants seem seldom to be affected by drought. Seedlings are, however much more susceptible, and may perish during prolonged periods of dry weather.

VI. Structure and physiology

(a) MORPHOLOGY

Cytological distinctions are present between the palisade cells of the upward-pointing and horizontal leaf segments (Hegi Fl. **VI. 4.**), with the former being longer and particularly chlorophyll-rich. This observation has been confirmed on British material.

Stomata are present on both upper and lower leaf surfaces. On the basal leaves, stomatal densities range between 29 - 91 mm^{-2} (mean = 63 mm^{-2}) and 128 - 333 mm^{-2} (mean = 216 mm^{-2}) on the upper and lower surfaces respectively.

(b) MYCORRHIZA

Plants examined in November 1996 showed abundant evidence of colonisation by V-A mycorrhizal fungi.

(c) PERENNATION: REPRODUCTION

Normally classified as a biennial semi-rosette hemicryptophyte (although Huxley (1967) describes it as biennial to perennial), with reproduction entirely by seed. *C. eriophorum* takes two years to complete its life cycle when grown in garden conditions (nutrient-rich soil with no close neighbours), but field observations indicate that at least a three year period (and possibly often much longer) is normally needed in order to complete the life cycle.

(d) CHROMOSOMES

2n=34 in British plants (Fl. Br. Isl.) and on the continent (e.g. Strid and Tan 1991 and references therein).

(e) PHYSIOLOGICAL DATA

C. eriophorum has a lower growth rate than *C. vulgare* during the early stages of development after reaching the two true-leaf stage, achieving only 38% of the biomass of *C. vulgare* after 49 days growth in 9 cm pots. This suggests that *C. vulgare* may have a strong competitive advantage in agriculturally improved grasslands compared with *C. eriophorum*, perhaps accounting for its greater abundance even in calcareous areas despite apparently performing more poorly in terms of initial germination (IV(b)).

(f) BIOCHEMICAL DATA

Nothing appears to be known about the compounds present in *C. eriophorum*. Biochemical data for the related *C. vulgare* are provided by Klinkhamer and De Jong (1993).

VII. Phenology

Stem elongation normally begins during early June in southern England, and the first flower buds appear during June or the beginning of July. The first flowers appear in early to mid July, and fruit is formed during August or early September. Smaller buds in the lower leaf

axils may flower later in the season (September), although these do not generally appear to produce good seed.

VIII. Floral and seed characters

(a) FLORAL BIOLOGY

Florets tubular, hermaphrodite. The corolla comprises a tube 23-28 mm long expanding into an unequally five lobed limb 12-15 mm in total length, the limbs being 3.5-9 mm long. The five stamens are epipetalous, 14-17 mm long, the anthers being united into a cylinder 9.5-10 mm long with 5 teeth at each end, enclosing the central part of the style. The style measures 20-26 mm long. Flowers are visited by bumble bees and butterflies. The proboscis of the bumble bee must be at least 7-8mm long, in order to reach the nectar in the floret base (Knuth Poll **II.**). The flowers are reddish purple, with white flowered forms being rarely recorded by a number of authors (e.g. Hegi Fl **VI. 4.**; Rouy Fl **9.**; Willkomm and Lange 1870; Thompson 1912; Huxley 1967).

The pollen grain is spiny, circular to weakly 3-angled and 40-70 μm in diameter in polar view, circular to slightly ellipsoid in meridian view.

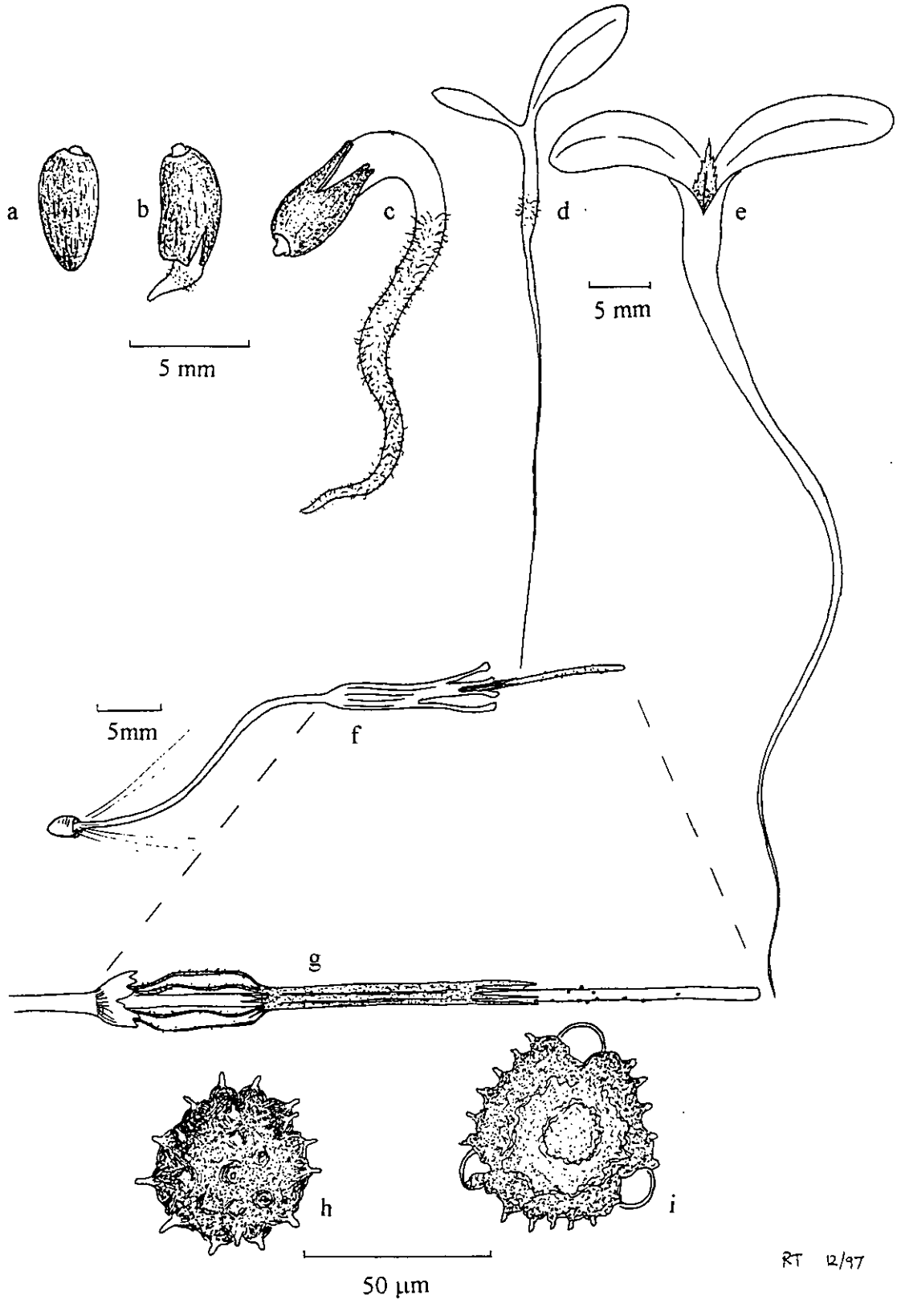


Figure 2. a: achene. b-e: seedling stages from germination to 14 days growth in the greenhouse. f: floret. g: part of floret with corolla tube removed, showing stamens, anthers and style. h-i: pollen grain, meridian and polar view.

(b) HYBRIDS

The hybrid *Cirsium eriophorum* x *C. vulgare* = *C.* x *grandiflorum* Kittel (*C.* x *gerhardtii* Schultz-Bip) has rarely been recorded in England from N. Somerset, N. Wilts, Dorset, N. Essex, Oxon, Cambs, S. Lincs and S.E. Yorks (Stace 1975). It is also known from Austria, Czechoslovakia, France, Germany, Switzerland, Hungary, Italy and the former Jugoslavia. It is intermediate in stem wingedness and capitulum characters and is partially fertile (Stace 1991). Two further hybrids (*C. eriphorum* (L.)Scop. x *C. palustre* (L.)Scop. = *C.* x *dominii* and *C. arvense* (L.)Scop. x *C. eriophorum* (L.)Scop. = *C.* x *semenii* Rouy) are known from Austria and Czechoslovakia, and from France respectively.

(c) SEED PRODUCTION AND DISPERSAL

(i) *Seed production*

The number of achenes produced per plant is highly variable, varying from plant to plant within a population and between populations. Salisbury (1952) notes that up to about 300 fruits may be produced per head (an observation that accords well with the results of this study), but observes that many fruits are eaten by beetle larvae. During the present survey 101 out of 102 freshly fruiting heads (i.e. those in which the majority of fruits had just reached maturity) showed signs of achene predation by insect larvae, and one head was found to contain 9 larvae. From a study of seven sites, the median number of undamaged fruits per head varied from 0 to 50, with a maximum observed number of 282 in one head. Figure 2 shows the frequency distribution of undamaged seeds per flowering head for *C. eriophorum* at Little Wittenham, Oxfordshire. The median number of fruits per head varies

greatly between populations ($p<0.001$ for the seven sites, Mood's median test), but Figure 2 shows the general form of the distribution which prevails at all sites. The number of flowering heads produced per plant is typically between 10 and 50. An estimate of the number of fruits usually produced per plant is therefore up to about 2500. Since seed predation due to insect larvae living in the thistle heads is almost universal, and typically acts to reduce the number of fruits released by at least 50% and often by more than 95%, it seems quite possible that the activities of insect larvae may act to control the abundance and distribution of *C. eriophorum* over at least parts of its range. Fruiting heads of *C. eriophorum* close during damp weather, and in such circumstances the population of insect larvae inside the heads may consume many achenes, destroying them before they can be dispersed when the heads reopen in drier weather. Fruits of *C. eriophorum* growing in areas with cooler summer temperatures may therefore mature more slowly, ripen later and be subject to greater retention during wet conditions, suffering higher consumption by insect larvae before they can be released.

Mean achene weights (n=100) vary from 7.9 - 10.3 mg. For collections made at approximately the same time, plants from near the central part of the British range (Little Wittenham, Berkshire) were found to have a significantly heavier mean achene weight than those from near the western extreme (Wick, Glamorgan), with a 100 seed weight of 9.9 - 10.3 mg compared with 7.9 - 8.3 mg ($p<0.01$, U-test). The western plants also produced fewer achenes per head (median=6, n=30) compared with the Berkshire ones (median=46, n=33) and generally fewer heads per plant (9-15 compared with 10-21).

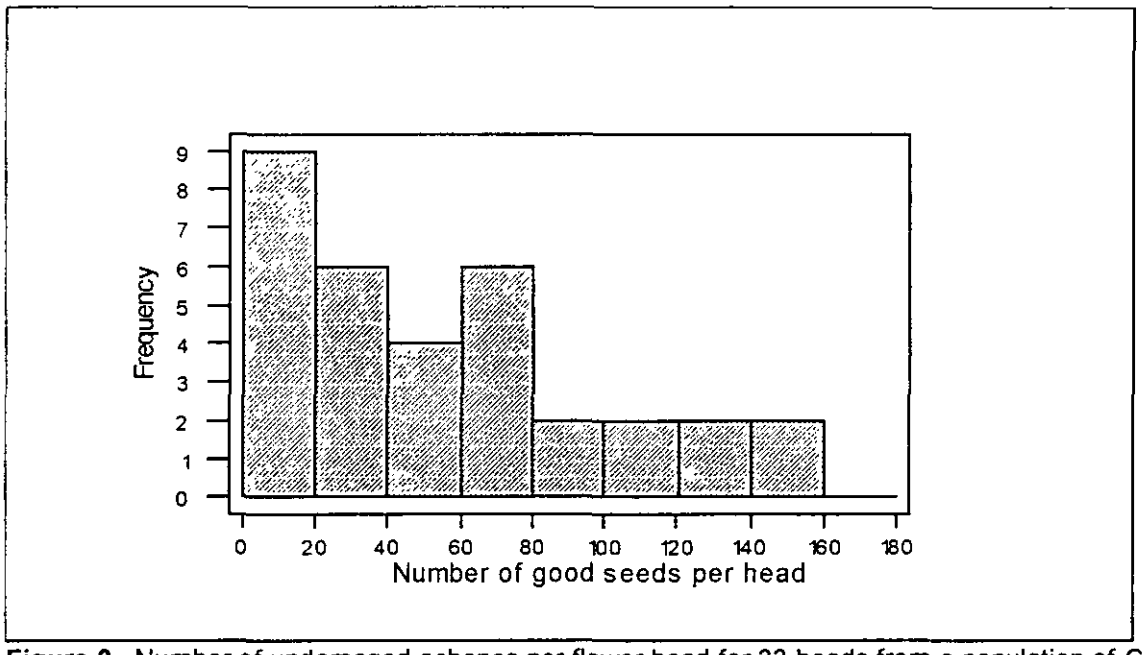


Figure 2. Number of undamaged achenes per flower head for 33 heads from a population of *C. eriophorum* at Little Wittenham, Oxfordshire.

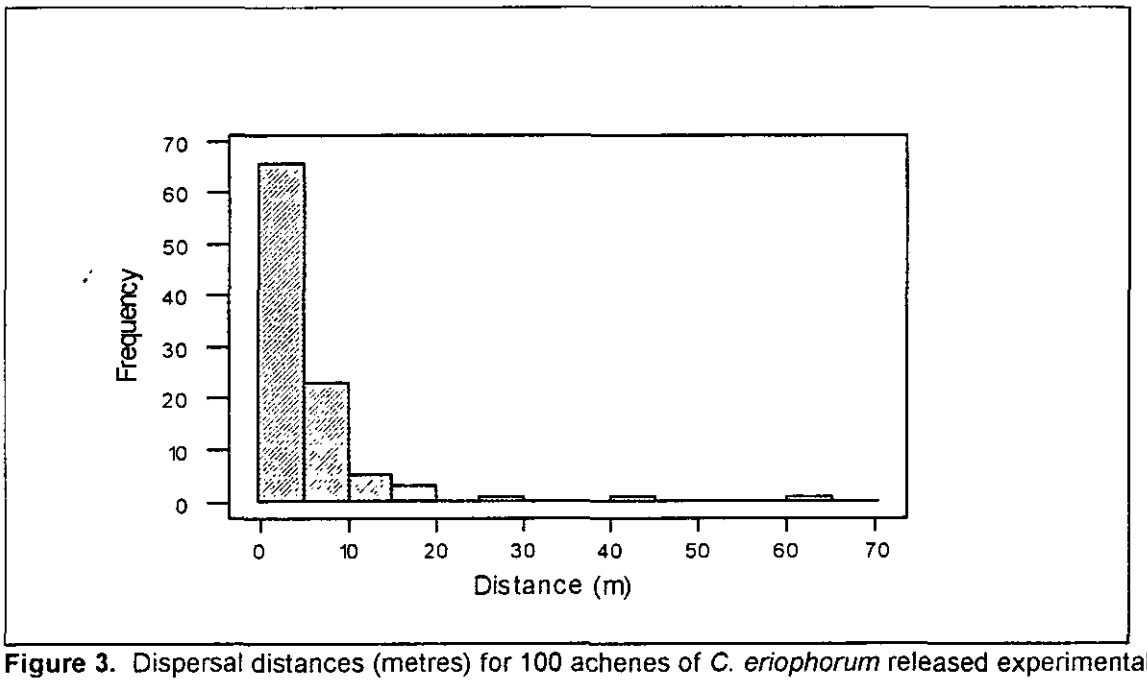


Figure 3. Dispersal distances (metres) for 100 achenes of *C. eriophorum* released experimentally at Little Wittenham, Oxfordshire.

(ii) *Seed dispersal*

Achenes are attached to a pappus, but field observations suggest that the pappus often becomes detached from the achene before it leaves the flower head. Even in cases where this is not so, most of the fruits appear to land within a distance of a few metres from the plant. Figure 3 shows the results of a dispersal experiment in which seeds of *C. eriophorum* were released during a period of natural seed dispersal at Little Wittenham, Oxfordshire. A comparison made at the same time revealed that *Cirsium vulgare* disperses seed significantly further than *C. eriophorum* (median = 4.9 m *vs.* 3.9 m, n_1=100, n_2=100, p<0.05 Mood's median test). The maximum dispersal distances recorded in this experiment were 60.5 m for *C. eriophorum* and >100 m for *C. vulgare*.

(iii) *Post-dispersal seed predation*

Some predation of seed due to small mammals has been observed. This appears to be very localised but may be severe, with upwards of 90% of seeds in a patch (*c.* 100 cm^2) being consumed.

(d) VIABILITY OF SEEDS: GERMINATION

Seeds have no cold requirement. Germination proceeds more rapidly in a dark environment, with the first signs of germination occurring after 3 days at 20^0C. Seed stored at room temperature for 1 month after collection and then germinated in the dark at 20^0C showed t_{50} of approximately 5 days. Germination in the dark and light (20^0C, 100 micro-einsteins $m^{-2}s^{-1}$) was 93% and 85% respectively. Seed stored for 12 months showed

germination of 81% in the dark. In nature, most germination appears to take place in the autumn although some seeds may germinate in the following spring.

(e) SEEDLING MORPHOLOGY

Cotyledons obovate, 15-20 x 8-12 mm. First true leaves lanceolate, some slightly spathulate, tomentose-wooly below, with weak buff coloured spines along margin.

IX. Herbivory and disease

(a) ANIMAL FEEDERS OR PARASITES

Freese (1995) recorded 11 phytophagous species from the stems and roots of *C. eriophorum*, but concluded that more extensive sampling would reveal many more. For all phytophagous species combined, Freese (*op. cit.*) calculated a mean number of 6.6 individuals per stem, and 93% of *C.eriophorum* plants was attacked. As in *C. vulgare*, a complex insect fauna is present in *C. eriophorum*, with herbivores and their associated predators and parasitoids, together with species which use the plants simply for the shelter they provide. In Britain and Europe, the flowers are commonly visited by bumble bees and butterflies. Wasps (*Vespa* spp) have frequently been observed to remove the 'wool' from small areas around the bracts, and to drink the liquid flowing from small incisions made in the bracts themselves. Table 2 lists the insect species recorded from *C. eriophorum*.

Table 2. Insect species recorded from *Cirsium eriophorum* in Britain and Europe.

Species	Data source	Ecological notes
COLEOPTERA		
Brentidae		
Acanephodus onopordi (Kirby)*	1	phytophagous on root collar
Cerambycidae		
Agapanthia dahli Richter**	1	larvae phytophagous/ ?facultatively entomophagous on stem
Chrysomelidae		
Cassida rubiginosa Müller*	6	larvae and adults externally on stems/leaves
Galeruca sp.*	6	larvae externally on stems/leaves
Cryptophagidae		
Micrambe lindbergorum (Bruce)	7	adults reared from seed heads
Curculionidae		
Cleonus piger Scopoli*	6	adults externally on stems/leaves
Larinus jaceae Fabricius**	6	larvae in flower heads/buds, adults on flower heads
Larinus scolymi Olivier**	6	adults on flower heads
Larinus sturnus Schaller**	6	larvae in flower heads/buds
Larinus turbinatus Gyllenhal**	6	larvae in flower heads/buds, adults on flower heads
Lasioderma sp.*	1	sapro/phytophagous on stem and possibly flower heads
Phyllobius oblongus Linnaeus*	6	adults visiting flowers
Mordellidae		
Mordellistena cf *parvuloides* Ermisch*	1	phytophagous on stem
Nitidulidae		
Brachypterus urticae (Fabricius)	7	adults feed on pollen (more usually on *Urtica dioica*)
Soronia grisea (Linnaeus)	7	adults reared from seed heads
Oedemeridae sp.*	1	phytophagous on stem
Scarabaeidae		
Cetonia cuprea Fabricius*	6	adults visiting flowers
DERMAPTERA		
Forficulidae		
Forficula auricularia Linnaeus	7	adults shelter in seed heads
DIPTERA		
Agromyzidae		
Melanagromyza aeneoventris (Fallén)*	1	larvae phytophagous in stem
Melanagromyza eriolepidis Spencer**	1	larvae phytophagous in stem

Table 2. Cont'd

Species	Data source	Ecological notes
Anthomyiidae		
Pegomyia steini Hendel	7	[probably as a larval miner in leaves or stems]
Cecidomiidae sp.*	6	larvae in flower heads
Muscidae		
Phaonia sp.*	1a	larvae predatory on larvae of *C. fraterna* and sciarids
Sciaridae sp.*	1	larvae phytophagous in stem
Syrphidae		
Cheilosia fraterna (Meigen)*	1	larvae phytophagous in roots/stems
Tephritidae		
Chaetostomella cylindrica (Robineau-Desvoidy)	3	larvae phytophagous in flower/seed heads
Terellia longicauda (Meigen)	3,7	larvae phytophagous in flower/seed heads
Terellia ruficauda (Fabricius)*	3	larvae phytophagous in flower/seed heads
Trypeta acuticornis Loew**	4	
Trypeta terebrans Loew**	5	
Urophora approximata Hering**	6	larvae phytophagous in flower/seed heads
Urophora eriolepidis Loew**	4	
Urophora stylata (Fabricius)*	3	larvae phytophagous in flower/seed heads
Xyphosia miliaria (Schrank)	3	larvae phytophagous in flower/seed heads
HEMIPTERA		
Tingidae		
Tingis cardui (Linnaeus)*	6	larvae and adults externally on stems/leaves
HYMENOPTERA		
Apidae		
Bombus lapidarius Linnaeus	7	adults visiting flowers
Megachile lagopoda Linnaeus	4	[probably a flower visitor]
Braconidae		
Aphaereta cf *tenuicornis* Nixon*	1a	larvae endoparasitic in *C. fraterna* larvae
Blacus exilis (Nees)*	1a	larvae endoparasitic in *Lasioderma* sp larvae
Brachistes sp**	1a	larvae endoparasitic in *M.* cf *parvuloides* larvae
Chorebus cf *brevicornis* (Thomson)*	1a	larvae endoparasitic in *M. aeneoventris* larvae and ?pupae
Glabracon fumipennis Thomson*	1a	larvae ectoparasitic on *C. fraterna* larvae
Glabracon hemiflavus Szépligeti**	1a	larvae ectoparasitic on *M. cribrella* larvae
Glabracon variator (Nees)*	1a	larvae ectoparasitic on *C. fraterna* larvae
Habrobracon hebetor (Say)*	1a	larvae ectoparasitic on *M. cribrella* larvae
Lucobracon erraticus Wesmael*	1a	larvae ectoparasitic on *M.* cf *parvuloides* larvae
Schizoprymnus sp.*	1a	larvae probably endoparasitic in *M.* cf *parvuloides* larvae
Eucoilidae		
Diglyphosema conjugens Kieffer*	1a	larvae endoparasitic in *M. aeneoventris* larvae and ?pupae

Table 2. Cont'd.

Species	Data source	Ecological notes
Eurytomidae		
Eurytoma centaureae Claridge*	1a	larvae ectoparasitic on *M. aeneoventris* larvae
Ichneumonidae		
Acaenitus dubitator (Panzer)*	1a	larvae endoparasitic in *C. piger* larvae/pupae
Diadegma erucator Thomson*	1a	larvae endoparasitic in *M. cribrella* larvae
Lissonota digestor Thunberg*	1a	larvae endoparasitic in *G. flavago* larvae
Phygadeuon sp.*	1a	larvae endoparasitic in *C. fraterna* larvae
Pteromalidae		
Chlorocytus sp.*	1a	larvae probably ectoparasitic on *A. dahli* eggs
Chlorocytus longicauda (Thomson)*	1a	larvae ectoparasitic on *M. aeneoventris* eggs
Chlorocytus spicatus (Walker)*	1a	larvae ectoparasitic on *M. aeneoventris* eggs
Pteromalinae sp*	1a	larvae endoparasitic in sciarid larvae
Sphegigaster intersita Graham*	1a	larvae endoparasitic in *M. aeneoventris*
Sphegigaster nigricornis (Nees)*	1a	larvae endoparasitic in *M. aeneoventris*
Stenomalina gracilis Walker*	1a	larvae ectoparasitic on *M. aeneoventris* larvae
Syntomopus incisus Thomson*	1a	larvae endoparasitic in *M. aeneoventris*
Syntomopus incurvus Walker*	1a	larvae endoparasitic in *M. aeneoventris*
Trichomalus cf *gynetelus* (Walker)*	1a	larvae ectoparasitic on *A. onopordi* larvae
Vespidae sp.	7	adults attacking phyllaries
LEPIDOPTERA		
Alucitidae		
Aciptilia nephelodactyla Ev[ersmann?]**	6	larvae externally on stems/leaves
Hesperidae		
Thymelicus lineola (Ochsenheimer)	7	adults feeding at flowers
Thymelicus sylvestris (Poda)	7	adults feeding at flowers
Noctuidae		
Gortyna flavago (Denis & Schiffermüller)*	1	larvae phytophagous on roots
Nymphalidae		
Argynnis sp.*	2	[probably adult feeding at flowers]
Cynthia cardui (Linnaeus)*	6	larvae externally (probably phytophagous) on stems/leaves
Vanessa atalanta (Linnaeus)	7	adults visiting flowers
Oecophoridae		
Agonopteryx propinquella (Treitschke)*	6	larvae mining leaves
Pyralidae		
Myelois cribrella (Hübner)*	1	larvae phytophagous in flower heads/stems
Phycitodes binaevella (Hübner)*	6	larvae in flower heads/buds

Table 2. Cont'd.

* British species recorded from *C. eriphorum* in Europe, but not yet in the British Isles.

** Insect species not recorded from Britain

Sources

1	:	Freese (1995)
1a	:	Freese (1995) - parasitoid reared from invertebrate host species known to occur in C. eriophorum, although actual specimens from which they were reared may have been obtained from other Cirsium species.
2	:	Müller (1883)
3	:	White (1988)
4	:	Knuth (Poll. **II.**)
5	:	Hegi (Fl. **VI. 4.**)
6	:	Zwölfer (1965)
7	:	personal observation

(b) PLANT PARASITES

Lousley (1950) includes a record of *Orobanche reticulata* on *C. eriophorum*, although this rare plant cannot be considered an important parasite of *C. eriophorum* in Britain.

(c) PLANT DISEASES

Ellis and Ellis (1985) list *Puccinia cnici* Mart. (a rust, on living plants) and *Phomopsis cirsii* Grove (on dead stems and leaves) from *C. eriophorum*. The hyphomycete *Periconia cookei* Mason & M.B. Ellis has also been seen on dead stems of *C. eriophorum* from Croughton, Northamptonshire. Hegi (Fl **VI. 4.**) lists *Erysibe cichoriacearum* DC., *Puccinia caricis frigidae* E.Fisch., *Ophiobolus acuminatus* (Sow.) Duby and *P. cirsii eriophori* Jacky.

X. History

No remains are recorded from British deposits of any age (Godw. Hist.), although the fruits of *C eriophorum* are distinctive. First recorded in Britain by Lobelius in 1570 'Tomentosus Carduus Angliae.....Frequens in Angliae collibus strigosis agri Sommerseti juxta aedes...', Clarke (First Rec.).

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References

Anderson, P. and Shimwell, D. (1981). *Wild Flowers and other Plants of the Peak District.* Moorland Publishing.

Atlas of Britain and Northern Ireland. Clarendon Press. Oxford.

Burnat, E. (1931). *Flore des Alpes Maritimes.* Geneva.

Clapham, A.R., ed (1969). *Flora of Derbyshire.* Bemrose & Sons Ltd.

Davis, P.H. (1975). *Flora of Turkey and the East Aegean Islands.* Vol 5. Edinburgh University Press.

Dony, J.G. (1967). *Flora of Hertfordshire.* Hitchin Museum.

Edees, E.S. (1972). *Flora of Staffordshire.* David & Charles.

Ellenberg, H. (1986). *Vegetation Ecology of Central Europe* (English Trans. 1988). Cambridge University Press.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. and Paulißen, D. (1991). Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica*, **XVIII**, 1-248.

Ellis, M.B. and Ellis, J.P. (1985). *Microfungi on Land Plants.* Croom Helm.

Freese, G. (1995). The insect complexes associated with the stems of seven thistle species. *Entomologia Generalis*, **19**, 191 - 207.

Gillam, B. ed (1993). *The Wiltshire Flora.* Pisces Publications.

Good, R. (1948). *A Geographical Handbook of the Dorset Flora.* The Dorset Natural History and Archaeological Society.

Grose, D. (1957). *The Flora of Wiltshire.* Wiltshire Archaeological and Natural History Society, Devises.

Gulliver, R.L. (1990) The rare plants of the Howardian Hills, North Yorkshire, 1794-1988. *Watsonia*, **18**, 69 - 80.

Hayek, A. and Markgraf, F. (1931). *Prodromus Florae peninsulae Balcanicae.* Vol 2. Berlin.

Hooker, W.J. and Arnott, G.A.W. (1860). *The British Flora.* Longman, London.

Horwood, A.R. and Noel, C.W.F. (1933). *The Flora of Leicestershire and Rutland.* Oxford University Press.

Huxley, A. (1967). *Mountain Flowers.* Blandford Press.

Jermyn, S.T. (1974). *Flora of Essex.* Essex Naturalists' Trust Ltd.

Kent, D.H. (1992). List of Vascular Plants of the British Isles. BSBI, London.

Klinkhamer, P.G.L and De Jong, T.J. (1993). Biological Flora of the British Isles. Cirsium vulgare. *Journal of Ecology*, **81**, 177 - 191.

Linton, W.R. (1903). *Flora of Debyshire*. Bemrose & Sons Ltd.

Lousley, J.E. (1950). *Wild Flowers of Chalk and Limestone*. Collins New Naturalist.

Mannagetta, G.R.B. von. (1892). *Flora von Nieder-Osterreich.* Wien.

Perring, F.H., Sell, P.D., Walters, S.M. and Whitehouse, H.L.K. (1964) *A Flora of Cambridgeshire.* Cambridge University Press.

Petch, C.P. and Swan, E.L. (1968) *Flora of Norfolk.* Jarrold.

Pigott, C.D. (1968). Biological Flora of the British Isles. Cirsium acaulon. *Journal of Ecology*, **56**, 597 - 612.

Poldini, L. (1991). *Atlante Corologico Delle Piante Vascolari Nel Friuli-Venezia Giulia.* Udine.

Rackham, O. (1989). *The Last Forest.* J. M. Dent. London.

Ray, J. (1724). *Synopsis Methodica Stirpium Britannicarum* (1973 reprint). Ray Society, London.

Rodwell, J. ed (1992). *British Plant Communities, Volume 3. Grasslands and Montane Communities.* Cambridge University Press.

Salisbury, Sir E. (1952). *Downs & Dunes: their plant life and its environment.* London. G. Bell & Sons Ltd.

Simpson, F.W. (1982). *Simpson's Flora of Suffolk.* Suffolk Naturalists' Society.

Stace, C. (ed). (1975). *Hybridization and the Flora of the British Isles.* Academic Press.

Stace, C. (1991) *New Flora of the British Isles.* Cambridge University Press.

Strid, A. and Tan, K. (1991). *Mountain Flora of Greece.* Vol 2. Edinburgh University Press.

Thompson, G.M. (1922). *The Naturalisation of Animals & Plants in New Zealand.* Cambridge University Press.

Thompson, H.S. (1912). *Sub-Alpine Plants.* George Routledge & Sons Ltd.

Trist, P.J.O. (1979). *An Ecological Flora of Breckland.* EP Publishing.

Webb, C.J., Sykes, W.R. and Garnock-Jones, P.J. (1988). *Flora of New Zealand.* D.S.I.R. Christchurch, New Zealand.

White, I. M. (1988). Tephritid flies (Diptera: Tephritidae). *Handbooks for the Identification of British Insects* **10(5a)**,1-134.

Willkomm, M. and Lange, J. (1870). *Prodromus Florae Hispanicae.* Vol 2. Stuttgart.

Zwölfer, H. (1965). Preliminary list of phytophagous insects attacking wild cynareae (Compositae) in Europe. *Technical Bulletins of the Commonwealth Institute of Biological Control*, **6**, 81-154.

Appendix 2

Local species pool

Appendix 2. The local species pool

The local species pool (forbs only) and probability of occurrence in the grazing trial using the model developed in Chapter 3. An asterisk indicates that the probability was not calculated because one or more of the variables used in the model was not available for the species. Species marked in bold type are present in the grazing trial. See Chapter 3 for further explanation.

Species	Probability of occurrence
Achillea millefolium	0.65
Aegopodium podagraria	0.62
Agrimonia eupatoria	0.62
Allium vineale	*
Anacamptis pyramidalis	0.14
Anthriscus sylvestris	0.65
Anthyllis vulneraria	0.25
Arctium minus	0.66
Artemesia vulgaris	0.56
Asperula cynanchica	0.14
Astragalus danicus	0.03
Bellis perennis	0.78
Blackstonia perfoliata	0.14
Campanula glomerata	0.23
Campanula rotundifolia	0.43
Capsella bursa-pastoris	0.96
Carduus nutans	0.40
Carlina vulgaris	0.25
Centaurea nigra	0.69
Centaurea scabiosa	0.58
Centaurium erythraea	0.46
Cerastium fontanum	0.73
Cerastium glomeratum	0.57
Chaerophyllum temulentum	0.49
Chamerion angustifolium	0.64
Cirsium acaule	0.47
Cirsium arvense	0.65
Cirsium eriophorum	0.16
Cirsium vulgare	0.68
Clinopodium vulgare	0.44
Coeloglossum viride	0.07
Colchicum autumnale	0.08
Conopodium majus	0.45
Convolvulus arvensis	0.69
Crepis biennis	0.05
Crepis capillaris	0.63
Crepis vesicaria	0.51
Cruciata leavipes	0.23
Cynoglossum officinale	0.51
Dactylorhiza fuchsii	0.04
Daucus carota	0.60
Erigeron acer	0.13
Euphrasia officinalis	0.36
Filipendula vulgaris	0.16
Fragaria vesca	0.66
Galium aparine	0.65
Galium mollugo	0.60
Galium pumilum	0.04
Galium verum	0.61

Gentianella amarella	0.19
Gentianella germanica	0.04
Geranium columbinum	0.11
Geranium dissectum	0.67
Geranium molle	0.72
Geranium pratense	0.45
Glechoma hederacea	0.65
Gymnadenia conopsea	0.13
Helianthemum nummularium	0.38
Heracleum sphondylium	0.69
Hippocrepis comosa	0.16
Hypericum perforatum	0.65
Hypochaeris radicata	0.58
Iberis amara	0.04
Inula conyza	0.16
Knautia arvensis	0.57
Lamium album	0.84
Lathyrus pratensis	0.68
Leontodon autumnalis	0.60
Leontodon hispidus	0.65
Leontodon taraxacoides	0.35
Lepidium campestre	0.11
Leucanthemum vulgare	0.66
Linaria vulgaris	0.57
Linum catharticum	0.50
Listera ovata	0.50
Lotus corniculatus	0.69
Malva moschata	0.29
Medicago lupulina	0.71
Onobrychis viciifolia	0.30
Ononis repens	0.40
Ononis spinosa	0.18
Ophioglossum vulgatum	*
Ophrys apifera	0.14
Orchis morio	0.13
Orchis ustulata	0.04
Origanum vulgare	0.25
Papaver dubium	0.48
Papaver rhoeas	0.70
Pastinaca sativa	0.57
Picris hieracioides	0.14
Pilosella officinarum	0.55
Pimpinella major	0.04
Pimpinella saxifraga	0.49
Plantago lanceolata	0.72
Plantago major	0.73
Plantago media	0.65
Polygala calcarea	0.08
Polygala vulgaris	0.36
Potentilla anserina	0.66
Potentilla erecta	0.52
Potentilla reptans	0.69
Primula veris	0.58
Prunella vulgaris	0.69
Pulsatilla vulgaris	0.03
Ranunculus acris	0.63
Ranunculus bulbosus	0.53
Ranunculus ficaria	0.56
Ranunculus repens	0.69

Reseda lutea	0.34
Reseda luteola	0.31
Rhinanthus minor	0.43
Rumex acetosa	0.62
Rumex conglomeratus	0.30
Rumex crispus	0.69
Rumex obtusifolius	0.71
Rumex sanguineus	0.52
Salvia horminoides	0.05
Sanguisorba minor	0.53
Saxifraga granulata	0.14
Scabiosa columbaria	0.24
Senecio erucifolius	0.41
Senecio jacobaea	0.69
Serratula tinctoria	0.13
Silaum silaus	0.16
Sonchus asper	0.59
Stachys officinalis	0.40
Stellaria graminea	0.53
Stellaria media	0.96
Succisa pratensis	0.53
Taraxacum officinale	0.65
Teucrium scorodonia	0.17
Thesium humifusum	0.05
Thymus polytrichus	0.34
Thymus puligioides	0.09
Torilis japonica	0.48
Tragopogon pratensis	0.56
Trifolium campestre	0.48
Trifolium dubium	0.75
Trifolium medium	0.17
Trifolium pratense	0.72
Trifolium repens	0.68
Urtica dioica	0.65
Veronica arvensis	0.73
Veronica chamaedrys	0.72
Veronica serpyllifolia	0.70
Vicia cracca	0.59
Vicia hirsuta	0.43
Vicia sativa	0.59
Vicia sepium	0.68
Vicia tetrasperma	0.25
Viola hirta	0.36